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Rates of Digestion of Different Prey in Atlantic Cod (*Gadus morhua*), Ocean Pout (*Macrozoarces americanus*), Winter Flounder (*Pseudopleuronectes americanus*), and American Plaice (*Hippoglossoides platessoides*)

J. Stevenson Macdonald[1] and Kenneth G. Waiwood

Marine Fish Division, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. E0G 2X0

and Roger H. Green

Department of Zoology, University of Western Ontario, London, Ont. N6A 5B7

Macdonald, J. S., K. G. Waiwood, and R. H. Green. 1982. Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). Can. J. Fish. Aquat. Sci. 39: 651 – 659.

Stomachs of ocean pout (*Macrozoarces americanus*), Atlantic cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*) were removed and dissected 5, 12, 20, and 30 h after the fish had fed voluntarily to test the evacuation rates of three different prey species. Two evaluation procedures were used: a visual index of recognizability, and a graphical analysis of percent of each prey recovered versus time since feeding. Three decay models were tested for goodness of fit to the evacuation data. The polychaete worms were the first to become unrecognizable, followed by amphipods. These species showed significantly different rates of evacuation when compared with the bivalves which were recognizable for the longest time. The exponential decay curve gave the best overall fit to the data. However, a linear model gave a good or better fit to the decay rate of the bivalve. The evacuation rates of different prey should be considered in estimating daily rations of fish in their environment.

Key words: digestion, stomach content, food organism, *Yoldia sapotilla*, *Tmetonyx cicada*, *Nephtys incisa*

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Les taux auxquels sont évacués trois différents types de proies ont été déterminés en enlevant et disséquant des estomacs de loquettes d'Amérique (*Macrozoarces americanus*), de

[1]Present address: Department of Zoology, University of Western Ontario, London, Ont. N6A 5B7.

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morues franches (*Gadus morhua*), de plies rouges (*Pseudopleuronectes americanus*) et de plies canadiennes (*Hippoglossoides platessoides*) 5, 12, 20 et 30 h après ingestion volontaire de nourriture. Deux méthodes ont servi à l'évaluation : un indice visuel de reconnaissance et une analyse graphique du pourcentage de chaque proie récupérée versus le temps écoulé depuis l'ingestion. Trois modèles d'extinction furent utilisés dans des tests d'adéquation des données d'évacuation. Les premières proies à devenir méconnaissables sont les vers polychètes, suivis des amphipodes. Ces espèces montrent des taux d'évacuation nettement différents de ceux des bivalves. Ces derniers sont reconnaissables le plus longtemps. Une courbe d'extinction exponentielle est en général celle qui s'ajuste le mieux aux données. Cependant, dans le cas des bivalves, un modèle linéaire s'ajuste également bien ou mieux au taux d'extinction. On devrait tenir compte des taux d'évacuation des différentes proies dans l'estimation des rations alimentaires quotidiennes des poissons dans leur environnement.

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VARIATION in the digestion pattern of different prey is an important variable in an evaluation of the diet composition, food preference, or consumption rate of wild fish. Estimates of daily ration based on gastric evacuation models require relatively accurate estimates of the rate of stomach emptying which is influenced by many factors, including prey type (reviewed by Windell 1978; Conover 1978). Unfortunately, information about prey-specific variation in digestion patterns is restricted to few predator–prey combinations, and many of these involve non-preferred or processed (e.g. dissected or frozen) prey items.

Evaluation of diet composition based on the percentage occurrence of prey in the stomach may be biased by differential rates of prey digestion (Hess and Rainwater 1939; Cailliet 1976; Gaare et al. 1977; Berg 1979). Conversion factors have been calculated to compensate for this.

This study was done to investigate the digestion pattern of three common prey (*Yoldia sapotilla*, *Tmetonyx cicada*, and *Nephtys incisa*) in four species of syntropic benthic fish (ocean pout (*Macrozoarces americanus*), Atlantic cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*)). Rate of elimination from the stomach was investigated by visual indexing of digestion stage to calculate the length of time the prey remained identifiable to species and the relationship between prey weight and digestion time.

Materials and Methods

Ocean pout (40.5–66 cm), Atlantic cod (32.5–45 cm), winter flounder (21.5–37.1 cm), and American plaice (16.8–31.8 cm) were collected by otter trawl from Passamaquoddy Bay during April–May 1980. They were transported to the St. Andrews Biological Station and held in 300-L-circular holding tanks which were supplied with a constant flow of salt water. The fish were held at ambient temperature (5–10°C) and salinities (28–31‰) for a minimum of 3 wk before being introduced to experimental tanks. They were fed a pelleted diet consisting of squid (26%), winter flounder (26%), rock crab (12%), herring meal (29%), herring oil (6%), vitamin package (0.75%), and sodium carboxymethyl cellulose (0.25%). Injured fish or fish that did not feed were excluded from subsequent experiments. At the beginning of each experiment, two fish of one species were placed in each of eleven 120-L-circular tanks and kept there for 9 d. A natural photoperiod was adopted and the water temperature was maintained at 6.25 ± 0.3°C during the experiment. Fish were given the above diet once daily (09:00–10:00) and were used experimentally once they fed voluntarily.

On the 1st day of a trial, each fish was fed one or more pellets containing one or more of the following prey species: *Y. sapotilla* (Bivalvia, 0.5–2 cm), *T. cicada* (Amphipoda, 0.5–1.0 cm), and *N. incisa* (Polychaeta, 2.0–8.0 cm). Care was taken to incorporate the entire, uncrushed, prey item into the pellet. These prey were collected from Passamaquoddy Bay with a 1.3-m-scallop dredge lined with fine mesh. The food items were frozen and stored at −20°C. The number of prey placed in each pellet varied as a result of differences in the maximum pellet size that each species could consume. Ocean pout with relatively large mouths could eat large pellets containing three prey species, whereas winter flounder were fed several smaller pellets containing one or two prey items. The prey composition of each pellet consumed by each fish was always recorded. Meal size as a percentage of body weight ranged from 0.5 to 3.3 for ocean pout, 0.96 to 2.14 for cod, 0.66 to 3.10 for plaice, and 0.64 to 3.19 for winter flounder. Five or six fish of each species (92 total) were killed at the following sampling times: 5, 12, 20, and 30 h after feeding. The fish remaining after 24 h were fed prepared food without the prey items, at the normal feeding time.

The alimentary tract was removed from each sampled fish and immediately placed in 5% Formalin saturated with Borax. Gut contents were exposed and prey remains were removed within 48 h of collection. The following data were recorded: (1) position of each prey within the gut (stomach or intestine), (2) condition of each prey using a four-category visual index, (3) prey length for estimating initial prey weight.

Prey remains were placed in aluminum weighing pans and dried to constant weight at 75°C.

In a separate experiment, the effect that frozen prey had on digestion rate was determined by feeding pellets containing freshly killed or live specimens of *N. incisa* and *Y. sapotilla* to ocean pout and cod. The fish were killed 5 and 20 h later. One-way ANOVA was used to test the effect of freezing on the indices of digestion and on the rate of weight loss of the prey with time. Only *Y. sapotilla* found in cod killed at 5 h showed significantly lower indices of digestion for the fresh as opposed to the frozen specimen ($P < 0.05$). However, both frozen and unfrozen *Y. sapotilla* could be keyed to species up

TABLE 1. Indices describing process of digestion from fresh to unrecognizable for each predator–prey combination.

	Y. sapotilla	*T. cicada*	*N. incisa*	Index no.
Pout, cod, flounder, and plaice	Shell fresh, foot and viscera undigested, shell surface unscratched	Fresh animal, color of body and eye intact	Fresh animal, color and setae distinct	1
Pout, flounder	Foot and mantle digested	Color of body and eyes paled	Setae attached to body but not in orderly rows — disorganized	2
Cod, plaice	Shell surface becoming scratched and opaque	Color of body and eyes paled	Setae attached to body but not in orderly rows — disorganized	2
Pout	Viscera digested	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
Cod	Foot and mantle digested	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
WF	Shell surface becoming scratched and opaque	Some appendages missing (often the antennae)	Viscera cleared from body leaving clear integument holding patches of setae	3
Plaice	Foot and mantle digested	Viscera digested from carapace, carapace brown and clear	Viscera cleared from body leaving clear integument holding patches of setae	3
Pout	Shell broken to unrecognizability	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
Cod	Shell totally opaque, very thin	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
WF	All viscera digested	Viscera digested from carapace, carapace brown and clean. Often broken	Clumps of setae attached to remnants of integument	4
Plaice	All viscera digested, shell very thin often with holes and ragged edges	Animals broken up	Clumps of setae attached to remnants of integument	4

to 30 h after feeding. The freezing effect was only significant at the early index categories where recognizability was not a problem. Ocean pout killed at 20 h digested the frozen *Y. sapotilla* significantly faster than the fresh ones ($P < 0.05$). Previously frozen *N. incisa*, fed to the cod killed at 20 h after feeding and to the ocean pout killed at 5 h after feeding, also lost weight significantly faster than did fresh ones ($P < 0.05$; ANOVA after arc sine transformation of the data). There were no significant differences between the fresh and frozen prey of any of the other eight predator–prey vs. time combinations. Because freezing has a similar but limited effect on both prey items tested, we believe that our results are valid.

Results

Evacuation Rates as Described by Average Indices of Digestion

Each category in Table 1 describes a stage in the digestion of a specific taxonomic feature which is required to key the animal to species (Gosner 1971). Digestion of *N. incisa* followed the same pattern in all predators. Similarly, the digestion pattern of *T. cicada* differed among predators only in that the viscera was digested and the appendages became detached earlier in the plaice compared with the other predators. Two digestion patterns occurred for *Y. sapotilla*. Ocean pout digested the viscera with little damage to the shell. The cleared valves can be seen in the rectum. On the other hand, cod digested the entire shell in the stomach, rarely letting any of it pass to the intestine in a recognizable state. Digestion of *Y. sapotilla* by winter flounder and plaice was similar to that by cod as it involved the decay of the entire shell. However, unlike the cod, the valves were often passed to the intestine before decaying completely.

The average index of digestion at each sacrifice time described the progression towards unidentifiability of the three prey species in each of the four predators (Fig. 1). In all four predators *N. incisa* was digested most rapidly to an unrecognizable state. This occurred after 20 h in the plaice and before 5 h in the three other predators. *Yoldia sapotilla* was identifiable at least 30 h after consumption in all four predators. *Tmetonyx cicada* was digested at an intermediate rate in all predators except the cod, where it could be identified 30 h after feeding.

The rate of passage of prey from stomach to intestine varied among predator and prey species (Fig. 1). All prey left the ocean pout stomach quickly and in a relatively undigested condition. For example, 50% (by numbers) of *Y. sapotilla*,

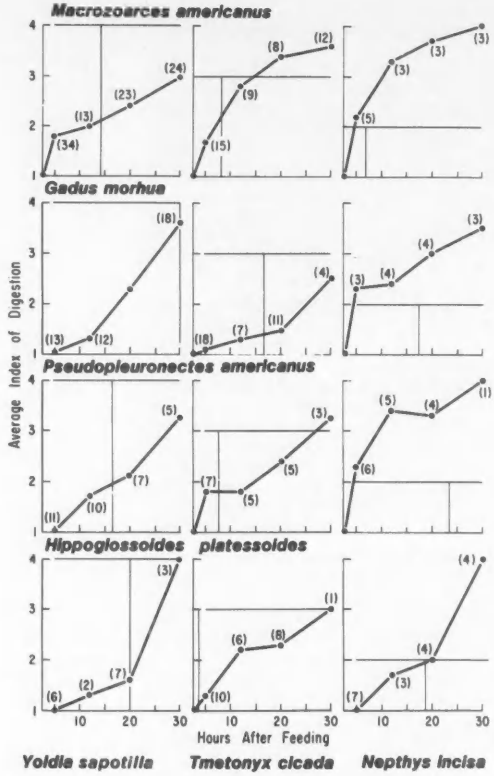

FIG. 1. Average index of digestion related to time after feeding for each of the three prey types digested by each of the four predator species. The horizontal lines represent the value of the index beyond which *Yoldia*, *Tmetonyx*, and *Nephtys*, respectively, cannot be identified to species. The vertical lines are the times at which 50% of each prey passes from the stomach to the intestine in each predator. Numbers in parentheses refer to the number of prey recovered at each time.

T. cicada, and *N. incisa* were evacuated from the stomach within 15, 8, and 7 h, respectively. For cod, the corresponding values were 30 h for *Y. sapotilla*, and 17 h for *T. cicada* and *N. incisa*. Food left the stomach of plaice and winter flounder at a rate similar to that observed for ocean pout with the exception of the slower passage of *N. incisa* (Fig. 1). There was a tendency for *Y. sapotilla* to remain in the stomach longer than the other two prey. This was found in all predators, but was most noticeable in cod and ocean pout (Fig. 1).

Generally, the rate of passage to the intestine was the most important factor affecting identifiability for *Y. sapotilla* and *T. cicada*. *Nephtys incisa* tended to decay in the stomach before it passed to the intestine.

Evacuation Rates as Described by Percentage Weight Loss with Time

The length vs. dry weight measurements of the three species of prey were best described by the power function (Table 2). The mean ratio of dry weight of partially digested prey to their initial dry weight (as back-calculated from the power functions) decreases with time for all predator–prey combinations (Fig. 2). Linear, logarithmic, and logistic models applied to the data emphasize this (Fig. 3). Two-parameter models with no specified Y-intercept were originally fitted. Subsequently, better estimates of evacuation rate were found by fitting one-parameter models with percentage recovery at time zero set at 100. These were linear, $Y = 100 - bt$; logarithmic, $Y = 100e^{-bt}$; and the logistic,

$$Y = \frac{99.9}{1 + e^{-b}(t - t_0)}.$$

Deviations of Y-observed from Y-predicted, as back-calculated from the models, were tested against a null hypothesis of the linear equation passing through 100%. This gave a more meaningful test than with a null hypothesis of zero slope (Table 3). Negative values for all predator–prey combinations, except for *N. incisa* in the ocean pout, suggest that the logistic curve gave a poorer fit than the null hypothesis (the linear model). Similarly the logarithmic model gives negative or low positive r^2 values when fitted to the *Y. sapotilla* decay curves of the four predators. Possibly in these situations, the linear model gives at least as good a fit as the logarithmic model. In all other predator–prey situations the logarithmic model gives a higher r^2.

The r^2 values for the data from all predator–prey combinations, for each model, were tested using a paired t-test after they were transformed by the ranking method described by Fisher and Yates (1967). The only significant difference in fit was between the logarithmic and logistic models, with the logarithmic model giving the best fit ($P < 0.05$).

The slopes from the logarithmic model fitted to each of the 12 predator–prey evacuation curves (Fig. 3) were compared using a two-way ANOVA. There was no significant predator effect, but there was significant difference between the evacuation rates of *Y. sapotilla* and the other two prey species

TABLE 2. Relationships used to convert length measurements (L in mm) of partially digested prey into original prey dry weight (W in g).

Prey	Measurement	Power function	Multiple correlation coefficient (r^2)
Yoldia sapotilla	Length of valve	$W = 0.03101(L)^{2.821}$	0.99
Tmetonyx cicada	Length of notch in last pleon.	$W = 0.00991(L)^{2.77}$	0.87
Nephtys incisa	Length of body	$W = 0.00130(L)^{2.2628}$	0.81

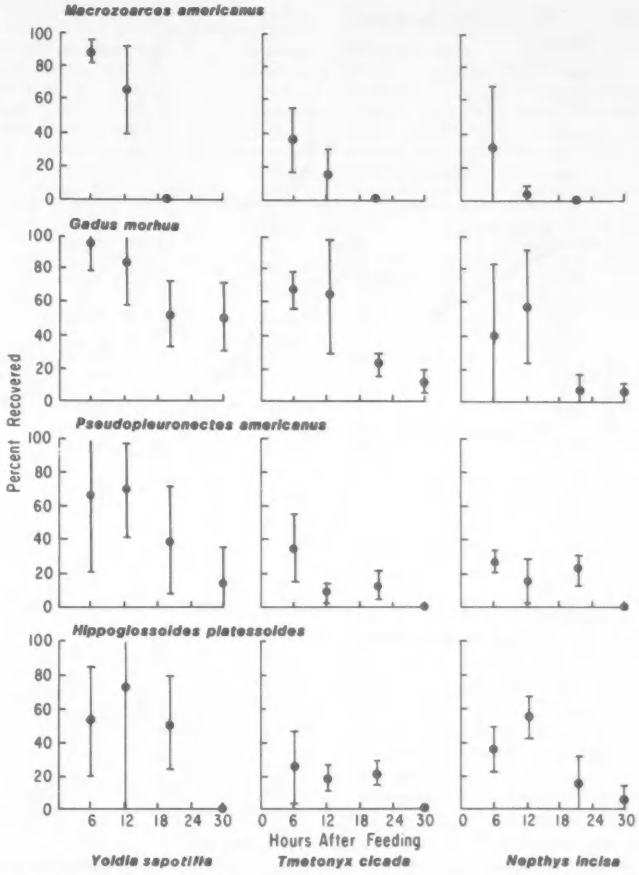

FIG. 2. Relation between percent by weight of prey recovered and time after feeding for different predator–prey combinations. Lines represent 95% confidence intervals about the mean.

($P < 0.05$). When slope values of all four predators are combined for each prey, the 95% confidence limits express the difference in evacuation rates between *Y. sapotilla* and the combined rates of *N. incisa* and *T. cicada* (Fig. 4).

Discussion

Evacuation rates as described by average indices of digestion

Ocean pout and cod have different patterns of food passage from the stomach. These patterns can be related to morphological differences in their alimentary tracts. The heavily muscularized cod stomach (Tyler 1973) breaks whole food and digests it before it is passed to the intestine. Ocean pout stomachs appear to be less muscularized and are primarily for storage. Molluscan valves and chitin are partially broken by the flattened pharyngeal teeth, are passed through the pyloric sphincter sooner, and are less digested than in cod.

The large-diameter intestine of the pout accepts larger and less-digested objects from the stomach than in the other species of fish examined. Experiments with plaice (Edwards 1971), cottids (Western 1971), and trout (Kionka and Windell 1972) suggest that narrow sphincters and intestines restrict the passage of large undigested objects from the stomach. This may also explain why large indigestible objects such as *Y. sapotilla* were expelled slower than other prey. A shorter, larger-diameter intestine may be an adaptation to retain large food longer and to allow more time for absorption. Longer retention in many herbivores and polychaete feeders results from increased intestine length (DeGroot 1971; Tyler 1973).

Increased absorptive area is achieved with pyloric ceca in the gadids and the pleuronectids. The thickened wall of the pout intestine may act in the same way in the absence of pyloric ceca. If larger objects pass into the pout intestine, pyloric ceca may be too constrictive to work efficiently.

Differences in rates of food passage among the four predators accounted for the major differences in decay pattern of the

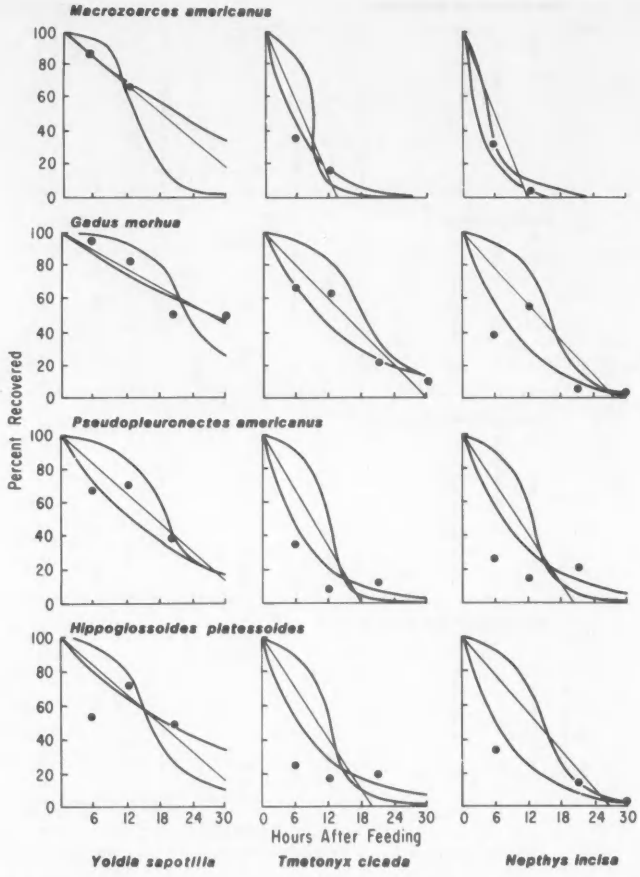

FIG. 3. Linear, logarithmic, and logistic models fitted to the data presented in Fig. 2 (the r^2 values are given in Table 3).

prey. From indices of digestion (Table 1), it appears that *Y. sapotilla* valves in cod and pleuronectids were retained in the stomach, having been broken more than those in pout. The stomach is more acidic than the intestine (Wilson 1972; Western 1971) and will digest a shell given sufficient time. Even though the gadids and pleuronectids appear to consume bivalves in nature (Frame 1974; Arntz 1974, 1977), this long retention time may make them a subtoptimal food. Any factor that slows evacuation rates slows food uptake rates and therefore prevents maximum growth (Vahl 1979). *Yoldia sapotilla* was not reported as a major food item for winter flounder or cod by Tyler (1972). Cod and pleuronectids have been observed by us and by Bishop and Odense (1966) to shake mollusks from their shells.

The change in physical condition of various food items as digestion proceeds has been reported (Hess and Rainwater 1939; Hunt 1960; Western 1971; Tyler 1973, Jones 1974). Generally, their observations agree with our results. The greater the percentage of chitin or shell in a food item, the longer it remains recognizable, i.e. bivalves were digested slower than amphipods which were digested slower than polychaetes. Many polychaetes have cuticles that resist digestion (Tyler 1973). Although many empty *N. incisa* skins were found in the stomachs, they do not have sufficient taxonomic detail to permit identification to the species level.

Hess and Rainwater (1939) demonstrated that diet analysis can be biased by the differential digestion rate of prey. Their method of calculating factors to correct for different digestion rates was modified to include correction for different food passage rates of the prey (Table 4). We found that many prey items passed from the stomach before digestion rendered them unrecognizable (Fig. 1). The length of time each prey species could be recognized in the stomach of each predator species was divided into the time required for the slowest prey item (*Y. sapotilla*) to disappear from the stomach. The actual number of prey species found in the stomach can be multiplied by the correction factor to give an unbiased estimate of diet composition.

TABLE 3. Squared correlation coefficients (r^2) representing unexplained deviations of the actual Y value (percentage of prey weight recovered) divided by the total deviations from the corresponding value representing the null hypothesis, all subtracted from one. In this case, the null hypothesis is the linear model passing through a Y-interecept of 100%. Negative values result where the fit is poorer than the linear model. Positive values result when the fit is better.

	Log	Logistic
Ocean pout		
Yoldia	−2.815	−59.520
Tmetonyx	0.886	−2.240
Nephtys	0.880	0.920
Cod		
Yoldia	0.445	−4.060
Tmetonyx	0.245	−1.320
Nephtys	0.500	−0.486
Winter flounder		
Yoldia	−0.066	−2.070
Tmetonyx	0.814	−0.681
Nephtys	0.594	0.707
Plaice		
Yoldia	0.153	−1.150
Tmetonyx	0.595	−0.852
Nephtys	0.478	0.525

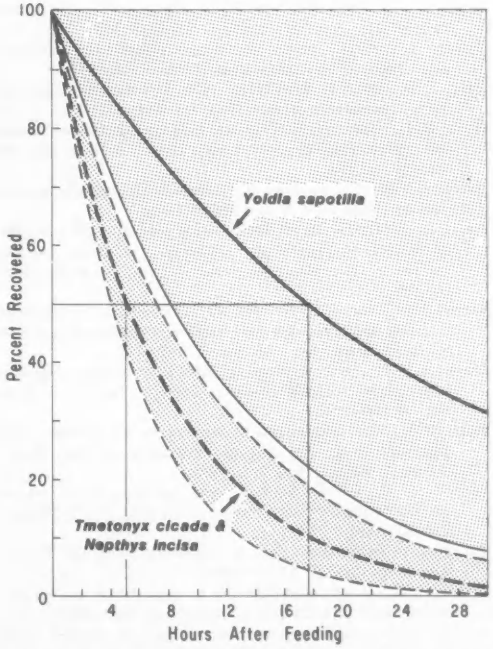

FIG. 4. Evacuation rates, using the logarithmic model, for *Yoldia sapotilla* and the combined decay of *Tmetonyx cicaca* and *Nephtys incisa* for all fish. Shaded areas represent 95% confidence limits of the model. The vertical lines to the 5.1- and 17.6-h marks show the time taken to achieve 50% evacuation by the *N. incisa*−*T. cicada* combination and *Y. sapotilla*, respectively.

TABLE 4. Correction factors for comparing the number of each of the three prey species within a single species of predator based on differential rates of evacuation or digestion (whichever causes the prey to disappear the fastest). Similarly, values in parentheses compare number of any one of the prey species among the four predators. Multiplication of the number of each prey observed in a particular predator's stomach by their correction factors will give comparable values of numbers of each species of prey eaten between prey species or between predator species.

	Prey		
	Y. sapotilla	*T. cicada*	*N. incisa*
Ocean pout	1.00	1.75	3.10
	(2.14)	(2.06)	(4.33)
Cod	1.00	1.82	6.70
	(1.00)	(1.00)	(4.33)
Winter flounder	1.00	2.20	3.67
	(1.82)	(2.06)	(4.33)
Plaice	1.00	5.63	1.08
	(1.50)	(4.71)	(1.00)

EVACUATION RATES AS DESCRIBED BY PERCENTAGE OF ORIGINAL PREY WEIGHT LOST OVER TIME

Percentage weight loss of food items over time is often used to describe digestion and to predict daily rations for fish (reviewed by Elliott and Persson 1978). Some researchers found no difference in depletion rate among different prey (e.g. Persson (1979) using zooplankton, amphipods, and chironomids; Windell (1966) using the natural prey of *Lepomis macrochirus*). Others, such as Jones (1974) using *Nereis*, *Nepthys*, and *Crangon* in cod and haddock, and Kitchell and Windell (1968) using damselfly naiads and mealworm larvae in pumpkinseed sunfish, found that prey type did affect rates of food depletion.

Many models have been fitted to evacuation data (Elliott and Persson 1978; Fänge and Grove 1979). There is difficulty in choosing the best one because several biological forces shape evacuation rate curves. Firstly, a lag occurs when the food enters the stomach (*Y. sapotilla* in ocean pout and cod, Fig. 2). Enzyme reactions are exponential and therefore start slowly (Jennings 1972). In experiments where a starvation period precedes the experiment, the digestive juices are not present when the food enters the stomach (Elliott 1972). The lag time also depends on the resistance of the food's surface and on the ratio of the food's surface area to volume (Windell 1967). Secondly, there is a period after the lag time when the digestive rate is maximal. The slope and shape of the line at this point is at least partially controlled by fat content of the food (Quigley and Meschan 1941; Windell 1967). Thirdly, the rate of evacuation will level off at a point determined by the percentage of indigestible material within the food, e.g. chitin (Battle 1935). Even when data are fitted to linear models, leveling off is often observed after 80 or 90% of the material is digested (Fig. 3; Daan 1973). Finally, it has not been considered that food may enter the intestine before it is fully digested. The stomach may act as a holding facility, emptying material to the intestine at a constant rate as intestinal space permits (e.g. ocean pout). Alternatively, the stomach may retain food until it has sufficiently mixed or broken down before passing it to the intestine (e.g. cod). Predictably,

one model will not fit all digestive relationships particularly well, given the many fish species and the many foods eaten.

The linear relation fits as well or better than the other two models when the prey is composed of a high degree of digestion-resistant material as in *Y. sapotilla* (Table 3). Despite its inherent ability to accommodate lag time, a steep rate of descent, and a leveling off with time, the logistic curve poorly described the gastric process; in some cases, lag times were not long enough and food items did not decay close enough to 0% to accept such a model (Fig. 3, Table 3). The exponential curve seemed to give a good fit for the faster digesting prey where there was less delay in commencement of digestion when the food entered the stomach (Table 3). For this reason, it successfully fitted data where prepared food or dissected natural food was used (Tyler 1970; Elliott 1972; Jones 1974). Cutting natural food, such as shrimp or fish, exposes the center of the food to the action of digestive enzymes and could potentially increase the rate of digestion.

The results of both the visual index and weight loss over time methods of evaluating digestion time partially support each other. The visual method indicates differences between all prey and some predators. The weight loss method shows differences between *Y. sapotilla* and the other two prey only (Fig. 4). However, the visual index method was not comparable to the weight-loss technique. The visual index is qualitative and true confidence limits cannot be applied. Also, digestion or weight loss of a prey item need not have any bearing on recognizability if the digestion has occurred to a portion of the animal that is not required to identify it.

The perception of the diet composition and of the consumption rates that fish have in the natural environment, and our models for describing the digestion processes, are affected by the variability in the digestion characteristics of each prey species. Analysis of consumption rates requires that the rate of weight loss by the prey be applied to the model which best describes the digestion process.

Acknowledgments

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Biological and Hydrographical Evidence for Pacific Equatorial Water on the Continental Shelf North of Vancouver Island, British Columbia

GRANT A. GARDNER[1]

Ocean Ecology Laboratory, Institute of Ocean Sciences, P.O. Box 6000, Sidney, B.C.

GARDNER, G. A. 1982. Biological and hydrographical evidence for Pacific equatorial water on the continental shelf north of Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. 39: 660–667.

Data from two cruises in April and November 1977 indicate the presence of Pacific equatorial water on the continental shelf north of Vancouver Island. Water with the general temperature/salinity characteristics of the California Undercurrent was found on the shelf at both times. Equatorial water formed ~30% of this deep-water mass, with Pacific subarctic water making up the remainder. Evidence for the presence of equatorial water was supported by the occurrence in the study area of six normally subtropical zooplankton species: *Mesocalanus tenuicornis*, *Lophothrix frontalis*, *Candacia bipinnata*, *Lucicutia flavicornis*, *Heterostylites longicornis*, and *Pleuromamma xiphias*. An increase in the proportion of equatorial water on the shelf, and a concomitant extension of the limits of distribution of oceanic zooplankters in the study area, both infer an intrustion of deep water onto the shelf during the period between the two cruises. This intrusion is probably a regular event with important ramifications for the zooplankton and fish communities of the area.

Key words: continental shelf, British Columbia, hydrography, California Undercurrent, zooplankton

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Les données recueillies lors de deux croisières, en avril et novembre 1977, indiquent la présence d'eau équatoriale du Pacifique sur le plateau continental au nord de l'île Vancouver. Aux deux époques, on a trouvé sur le plateau de l'eau possédant les caractéristiques de température/salinité générales du courant sous-marin de la Californie. Cette masse d'eau profonde est formée d'environ 30 % d'eau équatoriale, la balance étant de l'eau subarctique du Pacifique. La présence d'eau équatoriale est confirmée par l'occurrence, dans la région étudiée, de six espèces zooplanctoniques normalement subtropicales: *Mesocalanus tenuicornis*, *Lophothrix frontalis*, *Candacia bipinnata*, *Lucicutia flavicornis*, *Heterostylites longicornis* et *Pleuromamma xiphias*. Une proportion plus grande d'eau équatoriale sur le plateau et une extension concomitante des limites de distribution de zooplanctontes océaniques laissent toutes deux supposer une intrusion d'eau profonde sur le plateau dans l'intervalle séparant les deux croisières. Cette intrusion est probablement un phénomène régulier, avec importantes ramifications pour les communautés zooplanctoniques et ichtyologiques de la région.

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THE California Current system is well studied (see Hickey 1979 for a complete review), but still incompletely understood. The characteristics of northward flow between California and the Canadian west coast are particularly complex and unresolved (e.g. Ingraham 1967; Wooster and Jones 1970; Wickham 1975; Reed and Halpern 1976; Halpern et al. 1978). The primary current in this direction is the California Undercurrent, which in the south extends from the California coast to as far as 500 km offshore at depths below 200 m (Favorite et al. 1976) and which transports warm, low-oxygen equatorial water northwards (Tibby 1941). A narrower core is associated with this flow off southern Washington. The core is located near the shelf break, at about 200 m, and is less than 10 km from shore (Hickey 1979). The northward flowing Davidson Current, a seasonal surface phenomenon, is generally felt to be a manifestation of the California Undercurrent (Sverdrup et al. 1942; Burt and Wyatt 1964; Favorite et al. 1976).

The existence of these currents has been well documented as far north as the Strait of Juan de Fuca (e.g. Ingraham 1967; Cannon et al. 1975), but rarely examined farther north. Burt

[1]Present address: Department of Biology, Memorial University of Newfoundland, St. John's, Nfld. Canada, A1B 3X9.

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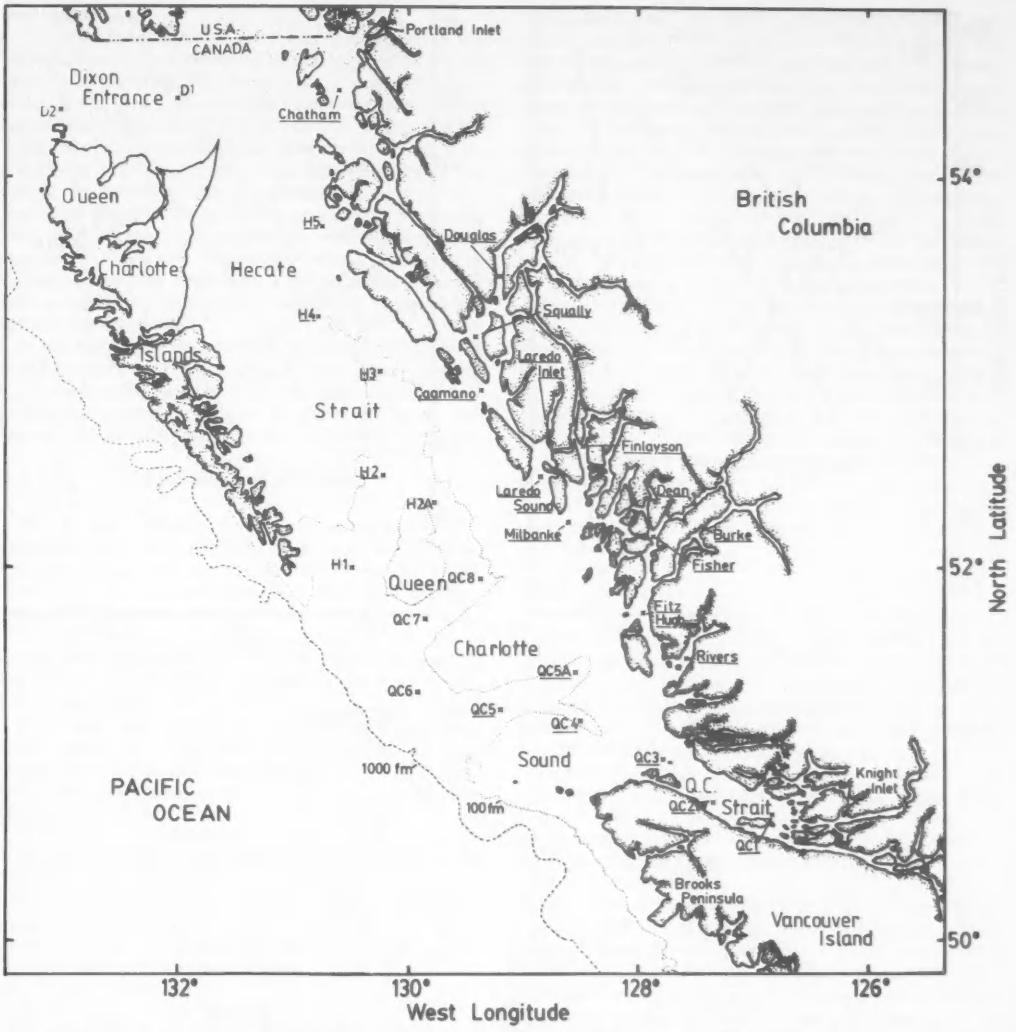
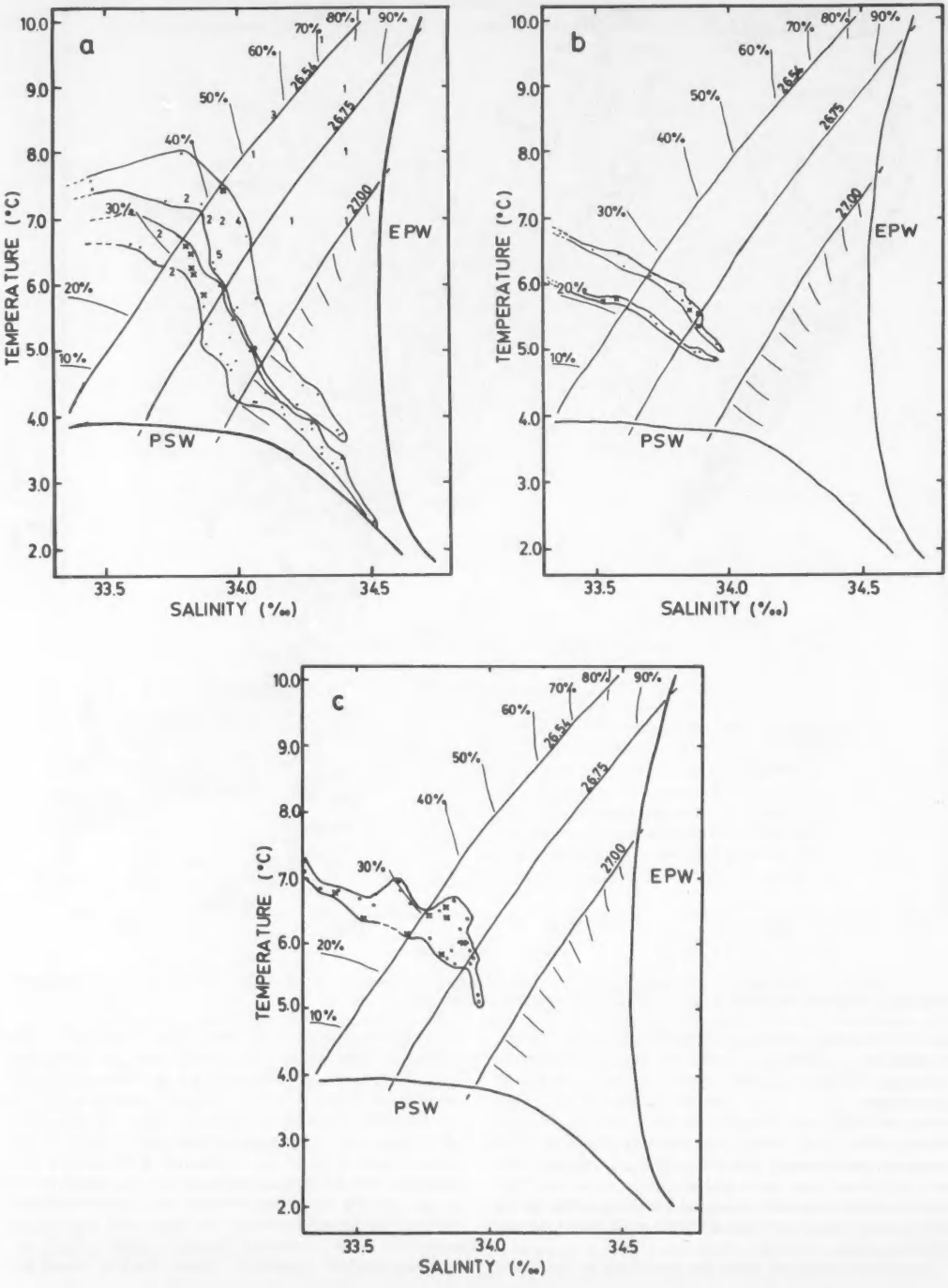


FIG. 1. Chart of the study area showing station locations: underlined stations were sampled on both cruises. Dixon Entrance was sampled in April only, while the remainder of the stations were sampled in November only.

and Wyatt (1964) report a drift bottle release off Astoria, Washington, and subsequent recovery over 2100 km north, at Afognak, Alaska. Reid (1965) shows a narrow tongue of low-oxygen water reaching from the equatorial Pacific north along the coast and eventually to the tip of the Aleutian Islands. The distribution of this low-oxygen water implies continuity of northward flow along the coast. Barber (1957) also implies at least occasional continuity of surface flow between California and Alaska, and describes some of the effects of this flow in the Hecate Strait and Queen Charlotte Sound regions.

Recent investigations along the west coast of Vancouver Island (Denman et al. 1982) show that at least part of the California Undercurrent may intrude onto the continental shelf. The strength and characteristics of northward flow between about 48°N and 50°N are currently under investigation (H. Freeland, Institute of Ocean Sciences, Sidney, B.C., personal communication). Toward the northern end of Vancouver Island (Fig. 1) the continental shelf narrows considerably, and the Brooks Peninsula juts out perpendicular to the shoreline and across the path of nearshore currents. North of the Brooks Peninsula, the continental shelf widens around the tip of Vancouver Island and opens to the broad, relatively shallow, expanse of Queen Charlotte Sound and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80%
90%
26.50
26.75
27.00
EPW
PSW

Hecate Strait.

The latter areas support locally important groundfish and herring fisheries, and provide a buffer between the Pacific Ocean seaward of the shelf break and a complex system of coastal inlets. Direct observations of cross-shelf movement of oceanic water into inlets do not exist. However, Gardner (1981) implies regular intrusions of water across the shelf, and Barber (1957) describes a mechanism for regular exchange of water between the offshore and the continental shelf zones. In addition, Stone (1980) describes a particularly interesting intrusion, into Knight Inlet, which carried a high proportion of unusual zooplankton species, almost all of southern origin. The implication is that on at least one occasion a significant proportion of equatorial water reached Queen Charlotte Sound.

In this paper, data from coastal waters north of Vancouver Island are used to examine the extent of influence of the California Undercurrent on the zooplankton community and hydrographic regime. I will show that Pacific equatorial water has a significant effect on the continental shelf in this region.

Materials and Methods

The data were collected from a series of stations (Fig. 1) visited on one or both of two cruises, in April and November 1977 (Ocean Ecology cruises 77/3 and 77/10, respectively). The cruises were primarily designed to investigate zooplankton distributions with respect to the hydrographic regime along the whole coast, and station positions were chosen accordingly. Nevertheless, 15 open water stations reaching from Queen Charlotte Strait to Dixon Entrance were sampled at least once each.

Zooplankton data are from vertical tows taken using a standard conical net constructed from nylon mesh netting (~350 μm mesh aperture) and equipped with a TSK flowmeter. For each station, temperature and salinity values were measured by bottle cast to standard depths. Details of data collection have been reported in Gardner (1980, 1981).

Except for a small number of taxa which could be identified only to genus, all copepods were sorted to species and selected species were sorted to copepodite stage. Where necessary, samples were split with a Folsom plankton splitter (McEwan et al. 1954); however, every effort was taken to minimize the extent of subsampling.

Results

Hydrographic Data

Off the coast of California, the core of the California Undercurrent is found at ~200 m and is associated with the 26.54-sigma-*t* surface (Wooster and Jones 1970). Data from the coasts of Washington, Oregon, and southern Vancouver Island show water with similar characteristics at the same depths (Ingraham 1967; Cannon et al. 1975; Wickham 1975; Halpern et al. 1978). Such data can be plotted on a temperature–salinity (T–S) diagram and shown in relation to 'pure' source water masses. If we assume that coastal water is derived from the Pacific subarctic and equatorial Pacific water masses (PSW and EPW, respectively), and further assume that mixing between these water masses occurs along surfaces of constant sigma-*t*, it is possible to estimate the percentage composition of the coastal water at a given site (e.g. Tibby 1941; Ingraham 1967; Reed and Halpern 1976). The percentage of equatorial water will be an index of the degree of northward transport via the California Undercurrent.

In both April (Fig. 2b) and May (Fig. 2c), deep water in Hecate Strait and Queen Charlotte Sound falls within the range of characteristics described for the California Undercurrent (Fig. 2a). The lines of percent composition on each figure suggest that in April the deep water on the shelf contained ~25–27% Pacific equatorial water. By November, the percentage of southern water had increased slightly, to ~26–35%. By the same criteria, water in Dixon Entrance, sampled only in April, contains 20–22% equatorial water. The only comparable data available (Institute of Oceanography, University of British Columbia, 1970) are included in Fig. 2a for comparison.

Zooplankton Data

Because of the widely arrayed station locations and the extensive zooplankton data required by the sampling strategy, it is more convenient here to consider only taxa that are primarily restricted to the exposed coastal stations. Such organisms are more likely to be of oceanic origin and hence associated with intruding oceanic water.

Eight of these taxa were identified to species and could be examined with respect to historical records of distribution (Table 1). Two of the species, *Neocalanus cristatus* and *Pleuromamma scutullata*, are from the Pacific subarctic, while the others are subtropical and have rarely been recorded north of about 48°N.

The 'southern' species have all been recorded off Oregon and Washington (Pearcy 1972), and except for *Mesocalanus tenuicornis* and *Lucicutia flavicornis* were all represented in the intrusion into Queen Charlotte Strait observed by Stone (1980). One of the species, *Candacia bipinnata*, was recorded as a rare immigrant into Strait of Georgia deep water (Fulton 1968), while another, *Heterostylites longicornis*, has previously been found in the Strait of Juan de Fuca (Chester et al. 1980; Gardner unpublished data). The northern species *N. cristatus* is also found occasionally inshore (e.g. Fulton 1968; Gardner 1981), but the remainder are more strictly oceanic, and with few exceptions have not been observed in protected waters nearshore. Of the species considered, only the two

FIG. 2. Hydrographic characteristics of continental shelf deep water. All figures show characteristic T–S curves for Pacific equatorial and subarctic waters (from Sverdrup et al. 1942), lines of equal sigma-*t*, and lines of approximate percent composition of water intermediate between the two source water masses. Figure 2a shows published data from the California Undercurrent (1 = Wooster and Jones 1970; 2 = Cannon et al. 1975; 3 = Wickham 1975; 4 = Ingraham 1967; 5 = Halpern et al. 1978) and data from Institute of Oceanography, University of British Columbia (1970). The latter data are contained within two T–S envelopes, an upper envelope containing data from three stations south of 48°N and a lower envelope containing data from six stations north of 48°N. Figure 2b and c show April and November hydrographic data, respectively. April T–S values fall into two distinct envelopes due to the Dixon Entrance data (the lower envelope). Most values are marked as dots, but data from (approx.) 200 m are marked as crosses.

TABLE 1. Distributional records in the Pacific Ocean for the eight species discussed.

Species	Distribution	Reference
Mesocalanus tenuicornis[a] (Dana, 1849)	Temperate and low latitudes	Brodsky (1950)
	North to ~48°N latitude	Davis (1949)
	Tropical and subtropical Pacific	Tanaka (1956)
		Mori (1964)
	San Diego region	Esterly (1905)
Candacia bipinnata (Giesbrecht, 1889)	Tropical and subtropical Pacific	Tanaka (1964)
	North to ~44°N latitude	Davis (1949)
	San Diego region	Esterly (1905)
Heterostylites longicornis Giesbrecht, 1889	Eastern Pacific between 14°N and 35°N latitude	Brodsky (1950)
Lophothrix frontalis Giesbrecht, 1895	Southern part of north Pacific (Bay of California; San Diego region) to ~35°N latitude	Brodsky (1950)
Lucicutia flavicornis (Claus, 1863)	30°N to 3°S latitude in the eastern Pacific	Brodsky (1950)
	Warm water regions	Tanaka (1963)
		Mori (1964)
	San Diego region; San Francisco Bay	Esterly (1905, 1924)
Pleuromamma xiphias (Giesbrecht, 1889)	Tropical and subtropical Pacific	Brodsky (1950)
	North to ~48°N latitude	Davis (1949)
	South of 44°N latitude	Chuchukalo (1973)
Neocalanus cristatus[a] (Kroyer, 1848)	North Pacific	Brodsky (1950)
		Davis (1949)
	Cold currents	Mori (1964)
Pleuromamma scutullata Brodsky, 1950	Northwest Pacific, Bering Sea	Brodsky (1950)

[a]The taxonomy of the Calanidae follows Bradford and Jillett (1974).

subarctic species (*N. cristatus* and *P. scutullata*) and two southern species (*M. tenuicornis* and *L. flavicornis*) were widespread and/or relatively abundant in the study area on at least one cruise. The others were found at no more than a few stations on either cruise.

The distribution of the four widespread oceanic species in April and November (Table 2) includes both open water and inshore occurrences to facilitate comparison of distribution patterns with respect to possible intrusions of oceanic water. All four species were more widely distributed and/or in higher concentrations in November than April. *Lucicutia flavicornis*, which was not seen at all in April, was observed at two open water and two unprotected inshore stations in November. The distribution of *N. cristatus* did not change appreciably at open water stations, but the species was found at 11 inshore stations in November versus 8 in April. Similarly, *M. tenuicornis* was more widely distributed inshore in November and was also present in higher numbers whereas *P. scutullata*, while not obviously differing in distribution, increased in concentration between the two cruises.

Discussion

HYDROGRAPHY

Barber (1957) described a seasonal onshore and offshore movement of bottom water in Queen Charlotte Sound and attributed it to changes in wind-induced surface currents. However, he did not consider either the source or the composition of the inflowing deep water. My hydrographic data suggest that the deep water on the shelf is composed of a significant proportion of equatorial water. The increase in the proportion of equatorial water on the shelf between April and November infers an influx, between the two cruises, of oceanic water containing a large component of EPW. This is consistent with Denman et al. (1982) and Freeland (personal communication), who have observed such water transported onto the shelf at lower latitudes during summer.

The estimated percentages of EPW in shelf bottom water are consistent with offshore hydrographic data collected by Gilfillan in March 1969 (Institute of Oceanography, University of British Columbia, 1970). Gilfillan's data (Fig. 2a), from a line of stations ~100 km seaward of the shelf break and stretching from Dixon Entrance to the coast of California, show a core of water at about 200 m with hydrographic characteristics consistent with published observations of the California Undercurrent. North of about 48°N, equatorial water makes up ~20–32% of this core. South of 48°N, off the coasts of Washington and Oregon, the percentage of EPW is closer to 35–40% (cf. Ingraham 1967, who shows greater than 35% equatorial water at about 200 m at a station 75 km seaward of the Oregon coast).

Data for the intrusion into Queen Charlotte Strait described

TABLE 2. Occurrence of major oceanic species in April and November 1977. Station locations are as marked in Fig. 1; concentration is the mean of all stations where the species occurred, and is expressed as no./m^3. (QC = Queen Charlotte Sound or Strait, H = Hecate Strait, D = Dixon Entrance.)

Species	April	Concn.	November	Concn.
Subtropical				
Mesocalanus tenuicornis	QC3/4/5/5A H2/3/4/5 D1/2 Milbanke Finlayson Squally Chatham	1.40	QC3/4/5/5A/6/7/8 H1/2/2A/3/4/5 Rivers Fitz Hugh Milbanke Laredo Sound Caamano Chatham	3.44
Lucicutia flavicornis	—	—	QC3/8 H2A Milbanke Laredo Sound	0.24
Subarctic				
Neocalanus cristatus	QC3/4/5/5A/2 H2/3/4/5 D1/2 Milbanke Finlayson Laredo Inlet Squally Caamano Portland Inlet	0.48	QC4/8 H1/2/2A/3/4 Rivers Burke Dean Fisher Finlayson Milbanke Laredo Sound Laredo Inlet Caamano Douglas	0.13
Pleuromamma scutullata	QC5 H2 D1/2	0.15	QC5A/6/7 H1/2	0.66

by Stone (1980) also indicate the presence of equatorial water. Although Stone's Queen Charlotte station is too shallow and well mixed to estimate the percentage of equatorial water present, dissolved oxygen values associated with the intruding water were much lower than in the displaced water (3.67 mL/L as an average for the water column between 5 and 150 m in July 1975 versus 4.33 mL/L in June: calculated from data in Institute of Oceanography, University of British Columbia, 1976). One of the characteristics of EPW is a low dissolved oxygen content (Hickey 1979), and the reduction in in dissolved oxygen seen in Stone's data is consistent with a substantial influx of equatorial water onto the shelf and from there to Queen Charlotte Strait.

Dixon Entrance is similarly influenced by equatorial water, although to a lesser extent. The April data indicate that about 21% of the water present at the Dixon Entrance Station could be attributed to equatorial water (cf. 26% for Queen Charlotte Sound at the same time).

ZOOPLANKTON

The eight oceanic species were generally more widespread and often more numerous during the fall cruise. Such changes may be attributed either to in situ breeding or to immigration via an inflow of oceanic water. The rarer species (*C. bipinnata*, *H. longicornis*, *Lophothrix frontalis* and *Pleuromamma xiphias*) were present in such low numbers that the presence of a successfully breeding population on the continental shelf is unlikely. Of the more common species, *L. flavicornis* was not found at all in April, and *P. scutullata* was present in relatively low concentrations. *Neocalanus cristatus* is more common inshore, but its population declined between April and November while its distribution expanded. Gardner (1981) describes the population fluctuations of *N. cristatus* (as *Calanus cristatus*) in greater detail and indicates that they are more consistent with immigration by intrusion than with in situ breeding.

Only one of the species, *M. tenuicornis*, is sufficiently tolerant to be widespread and relatively numerous in open water on the shelf. Nevertheless, the only occurrence of *M. tenuicornis* at a station removed from direct contact with offshore water comprised only two individuals (Finlayson Channel, April 1977), and it is unlikely that the species has a self-sustaining population inshore. The absence inshore of early copepodite stages (younger than C IV) of all of the oceanic species further suggests that the populations are maintained by immigration rather than breeding.

The presence of zooplankton species characteristic both of

PSW and EPW suggests some admixture of these two source waters to form the intruding water mass, and further supports the concept of at least occasional flow of EPW as far north as Dixon Entrance.

IMPLICATIONS

In the absence of continuous data, even large-scale intrusions of oceanic water are difficult to observe directly, but are normally inferred in one of two ways. The presence inshore of normally oceanic zooplankters may be taken as evidence of an intrusion (e.g. Stone 1980; Gardner 1981), or temperature and salinity data collected over a time series may show replacement of one water type by another (e.g. Pickard 1975). The latter method is most definitive and also best known; however, 'indicator' species may be particularly useful if mixing processes have destroyed the physical evidence of intrusion, but some of the more tolerant oceanic species remain. Such species may survive for extended periods (e.g. 1 yr: Wiebe et al. 1976) despite greatly changed hydrographic conditions, but as long as they cannot actively reproduce, their populations will be maintained solely by immigration via intrusions.

Both hydrographic and zooplanktonic data from 1977 imply an intrusion of offshore water onto the continental shelf north of Vancouver Island and further indicate that a substantial proportion of the water on the shelf originated in the equatorial Pacific water mass. The influence of equatorial water lessened northwards, but was still apparent at Dixon Entrance.

These and other data (e.g. Institute of Oceanography, University of British Columbia, 1970, 1976; Stone 1980) indicate that the whole of the north coast adjacent to Queen Charlotte Sound, Queen Charlotte Strait, Hecate Strait, and Dixon Entrance is regularly affected by intrusions which contain a high proportion of equatorial Pacific water. The frequency of such intrusions is uncertain and cannot be predicted from the available data. Nevertheless, Barber's (1957) suggested mechanism would imply that some degree of intrusion occurs annually, and an intrusion is inferred in every summer for which adequate data are available. The intensity of this intrusion undoubtedly varies from year to year, in part in response to variations in the strength of coastal upwelling (e.g. Stone 1980), which may be an important controlling mechanism for movement of California Undercurrent water onto the shelf.

Regardless of their cause, such intrusions influence the resident zooplankton communities on the continental shelf and adjacent waters and may also have important ramifications for groundfish stocks (e.g. Barber 1957). The degree of influence and extent of the intrusions infers that they play a major role in the ecology of northern British Columbia waters. The movement of equatorial water onto the continental shelf will be a major component of that role.

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Particle-Size-Conversion Efficiency and Total Animal Production in Pelagic Ecosystems

UWE BORGMANN

Department of Fisheries and Oceans, Great Lakes Biolimnology Laboratory, Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

BORGMANN, U. 1982. Particle-size-conversion efficiency and total animal production in pelagic ecosystems. Can. J. Fish. Aquat. Sci. 39: 668–674.

A method is described for defining conversion efficiency in pelagic ecosystems on the basis of particle size, rather than trophic level. This permits calculation of a size-corrected biomass function which can be used to describe total animal production by taking into account biomass losses resulting from carnivorous feeding in multitrophic level systems. This, in turn, permits the determination of potential fish production, for any given size fish, from experimental data on zooplankton production using simple equations. Little knowledge of trophic interactions is required. The potential fish production resulting from microzooplankton production in the Burlington Canal is calculated.

Keywords: conversion efficiency, production, pelagic ecosystem, particle-size spectrum

BORGMANN, U. 1982. Particle-size-conversion efficiency and total animal production in pelagic ecosystems. Can. J. Fish. Aquat. Sci. 39: 668–674.

On trouvera dans l'article qui suit la description d'une méthode permettant de définir le rendement de conversion dans des écosystèmes pélagiques en se fondant sur la taille des particules plutôt que sur le niveau trophique. On peut ainsi calculer une fonction de biomasse corrigée quant à la taille pour décrire la production animale totale. Pour celà, on tient compte des pertes de biomasse résultant de l'alimentation carnivore dans des systèmes à multiples niveaux trophiques. Ceci à son tour permet de déterminer la production potentielle en poissons, de quelque taille que ce soit, à partir de données expérimentales sur la production zooplanctonique et à l'aide d'équations simples. Il n'est pas nécessaire de bien connaître les interactions trophiques. Nous calculons la production potentielle en poissons à partir de la production microzooplanctonique dans le canal de Burlington.

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ALTHOUGH measurements of the biomass production rates of individual pelagic species are now routinely made, estimates of production in entire ecosystems or even parts of ecosystems are more difficult to obtain. For the phytoplankton community, total production is usually simply the sum of the production of each of the individual species, as most phytoplankton do not consume other organisms. Animal production, on the other hand, results from consumption of both plants and other animals, and it is often difficult to determine who feeds on what and how much. For example, biomass production rates of natural populations of freshwater copepods, and factors influencing these rates, can rapidly be determined in relatively simple procedures which even permit crude estimates of ecological efficiencies (Borgmann et al. 1979). However, refinement of ecological-efficiency estimates for these copepods is confounded by the unavoidable presence of both herbivorous and carnivorous rotifers. Hence, complex species interactions are possible, and because the preferred food of the copepods (mainly cyclopoids) is not accurately known, and indeed is likely to change during the experiment as the copepods grow, the actual number of trophic steps involved is unknown.

Fortunately pelagic ecosystems have a unique feature which permits, to some degree, circumvention of the problem of direct determination of trophic level. As most plant production is by microscopic phytoplankton, pelagic herbivores are generally small, and production of large organisms usually results from the carnivorous feeding of progressively larger animals. Consequently, body size is a rough indication of trophic level. This property of pelagic ecosystems has contributed to the development of several models on the biomass size spectrum (e.g. Kerr 1974; Sheldon et al. 1972, 1977; Platt and Denman 1977, 1978; Silvert and Platt 1978, 1980) and has permitted estimation of fish production from primary production (e.g. Sheldon et al. 1977). These models, however, are not directly applicable to solving some of the problems encountered in experimental situations such as the one described above for copepods and rotifers.

In this paper, I propose a definition of conversion efficiency based on the efficiency of conversion of particles (organisms) from one size to another, rather than from one trophic level to the next. Many of the problems associated with solving complex equations for multispecies interactions can be avoided in this way. Furthermore, problems of defin-

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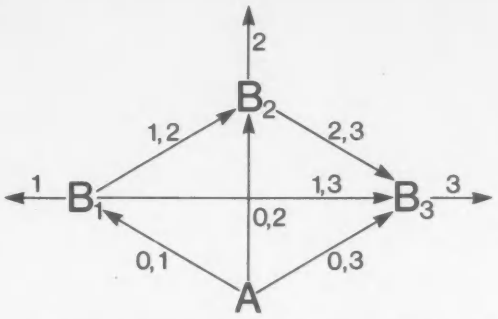

FIG. 1. Model for a hypothetical pelagic community of three animal species at increasing trophic levels (B_1, B_2, and B_3). Each pathway of flow of organic matter is indicated by two numbers except for nonpredation mortality rates which are indicated by single numbers. Phytoplankton, detritus, and other microorganisms are indicated by A.

TABLE 1. Equations for the rate of change in biomass for individual species and for the total biomass for the model in Fig. 1.[a]

(1)	$dB_1/dt = P_{0,1} - M_1 - C_{1,2} - C_{1,3}$
(2)	$dB_2/dt = P_{0,2} - M_2 + P_{1,2} - C_{2,3}$
(3)	$dB_3/dt = P_{0,3} - M_3 + P_{1,3} + P_{2,3}$
(4)	$dB_T/dt = \Sigma dB_i/dt = \Sigma P_{0,i} - \Sigma M_i + \Sigma(P_{ij} - C_{ij})$

[a] B_i = biomass of each animal species; P_{ij} = biomass production rates resulting from a given pathway; C_{ij} = food consumption rates along various pathways; M = mortality other than predation.

ing trophic level, especially for organisms which in nature may feed on several lower trophic levels, are eliminated. This permits analysis of experimental and field data on multiple trophic levels and makes possible predictions of potential production at higher trophic levels, calculations that would otherwise be much more difficult. An example is given.

Theory

Conventional Terminology and its Limitations

The problems encountered in analyzing production of entire pelagic animal communities can be demonstrated using a model such as shown in Fig. 1. The equations (1 to 4) describing the rate of change in the biomass of each species and the rate of change of the total animal biomass are given in Table 1. Although the model in Fig. 1 contains only three animal species, the equation for the rate of change in total biomass is written in a general form to include any number of species. As some species undergo large changes in size during development, the food organisms consumed may vary considerably and hence also the magnitude of the biomass flow through various pathways. The equation for the rate of increase in total animal biomass (equation 4) has three terms. The first is the rate of production resulting from consumption of food other than animal matter. The second term represents natural mortality which includes biomass losses other than

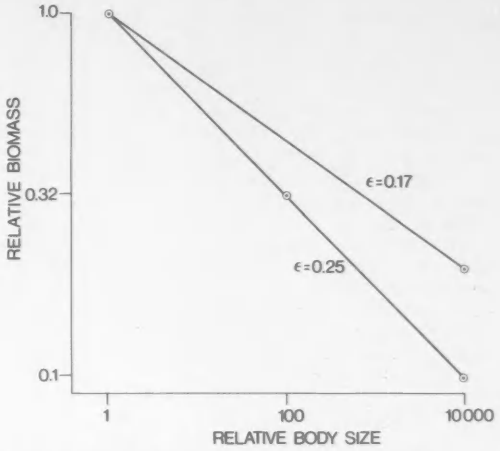

FIG. 2. Hypothetical examples of the logarithm of the biomass remaining after transfer through one or two trophic levels plotted against the logarithm of body size at each trophic level. The slope of the line (ϵ) gives the size-conversion efficiency. The upper line ($\epsilon = 0.17$) represents a single trophic step with a conversion efficiency (K_1, the conventional term for efficiency) of 20% and predator–prey size ratio of 10 000, whereas the lower line represents a two-trophic step food chain with each K_1 equal to 32% and predator–prey size ratios of 100.

predation. The third term indicates the rate of loss of biomass due to predation. It is this third term which is most difficult to deal with in solving for dB_T/dt. This term contains two coefficients, the ratio of which (P_{ij}/C_{ij}) is the efficiency of conversion of biomass (or energy) from one trophic level to the next, often designated by K_1. If this value is assumed to be constant, the third term in equation 4 can be simplified to $\Sigma P_{ij}(1 - 1/K_1)$. Unfortunately, the values of P_{ij} must still be determined in some way, and hence equation 4 is still difficult to apply.

Particle-Size-Conversion Efficiency

The solution and application of an overall equation for pelagic production, such as equation 4, can be greatly simplified by introducing a different definition of conversion efficiency (in place of K_1) which takes into account changes in organism size. The conversion efficiency from one particle (organism) size to another can be written,

$$(5) \qquad \epsilon = \frac{\log C_{ij}/P_{ij}}{\log W_j/W_i}$$

where ϵ is the particle-size-conversion efficiency, and W_j and W_i are the predator and prey sizes, respectively. This is shown diagrammatically in Fig. 2, where the logarithm of the initial biomass remaining is plotted against the logarithm of the relative particle size for two hypothetical situations, one with a conversion efficiency (P_{ij}/C_{ij}) of 20% and predator–prey size ratio of 10 000, and the other with an efficiency of

32% and predator–prey ratio of 100. The efficiency of conversion of particles from one size to a size 10 000-fold greater is better for the single-trophic step case, although not as different from the two-trophic step case as would occur if the efficiencies P_{ij}/C_{ij} were the same. A high slope (high ϵ) indicates a low efficiency and a low slope a high efficiency. The size-conversion efficiency, therefore, provides a means of comparing efficiencies of various food chains by correcting for differences in predator–prey size ratios and number of trophic levels.

The advantage of using particle-size-conversion efficiency (ϵ) in place of the conventional efficiency definition (K_1) in ecosystem modeling can rapidly be demonstrated. If ϵ for the major pathways is relatively constant, it then becomes possible to write a much simplified equation for the rate of total animal production. This is accomplished by first defining a size-corrected biomass (B^*) as follows

$$(6) \quad B_i^* = B_i W_i^{\epsilon}$$

where ϵ is the size-conversion efficiency. Replacing B_i with B_i^* in equations 1 to 4, the rate of change in the total size-corrected biomass becomes

$$(7) \quad dB_T^*/dt = \Sigma P_{0,i} W_i^{\epsilon} - \Sigma M_i W_i^{\epsilon} + \Sigma (P_{ij} W_j^{\epsilon} - C_{ij} W_i^{\epsilon})$$
$$= \Sigma P_{0,i} W_i^{\epsilon} - \Sigma M_i W_i^{\epsilon}.$$

The last term in equation 4 cancels out in equation 7 as a direct result of the definition of ϵ (equation 5). Hence, when biomass is expressed on a size-corrected basis, it is no longer necessary to consider biomass losses due to predation, and the rate of change in total size-corrected biomass is simply the total animal production (i.e. from nonanimal foods) less total nonpredation mortality.

Estimating Potential Fish Production

The concepts of size-corrected biomass and particle-size-conversion efficiency can be applied directly to the problem of estimating potential production of fish of any given size, especially under steady-state conditions for a food chain with negligible nonpredation mortality. For a chain $j = i + 1$ and therefore production at level i at steady state is given by

$$(8) \quad P_{(i-1)i} = C_{i(i+1)}.$$

If production is defined on a size-corrected basis, combination of equations 5 and 8 gives

$$(9) \quad P_{(i-1)i} W_i^{\epsilon} = C_{i(i+1)} W_i^{\epsilon} = P_{i(i+1)} W_{i+1}^{\epsilon} = F.$$

Hence, if all production at one trophic level is utilized by the next trophic level, at steady state the rate of production of size-corrected biomass at one trophic level is constant (F) and equivalent to the rate of production of size-corrected biomass at any other trophic level. If the production rate at any trophic level is known, F can be determined and the production at any other trophic level can be calculated from

$$(10) \quad P_{(i-1)i} = F/W_i^{\epsilon}.$$

Equation 10 need not be restricted to studies on food chains, but can also be used for food webs (e.g. Fig. 1) provided all the biomass flows through one or more species at a size W_i. In real systems, a maximum size exists for W_i, and equation 10 must therefore be used with caution for top predators, especially if no commercial harvesting or other exploitation of their production exists. The top predators may then have no real net production under steady-state conditions, except that required to offset natural mortality, and hence the value of ϵ must increase rapidly with body size as maximum size is approached.

Size-Conversion-Efficiency and the Biomass-Size Spectrum

At steady state, the shape of the biomass-size spectrum can readily be deduced from the above concepts and a knowledge of growth rates. If we again consider a food chain with insignificant nonpredation mortality, and rewrite production (P) in terms of the rate of production per unit biomass (p) times the biomass, equation 9 becomes

$$(11) \quad F = P_{(i-1)i} W_i^{\epsilon} = p_{(i-1)i} B_i W_i^{\epsilon}$$

where, as before, F is a constant. The production rate p can be related to body size using

$$(12) \quad p_{(i-1)i} = a W_i^{-n}$$

where a and n are constants. Combination of equations 11 and 12 gives

$$(13) \quad B_i = \frac{F W_i^{n-\epsilon}}{a}.$$

Hence, the biomass at any size is proportional to the size raised to the exponent $n - \epsilon$.

Estimates of Particle-Size-Conversion Efficiency

Application of the size-corrected biomass concept requires, first and foremost, an estimate of the particle-size-conversion efficiency, ϵ. Some estimates of ϵ obtained from published values of K_1 and predator and prey sizes, where available simultaneously, for carnivorous zooplankton are summarized in Table 2. Predator sizes were estimated from figures, tables, or the text and may be variable, especially for *Calliopus* (Dagg 1976). The only authors who actually calculated predator–prey size ratios were Corner et al. (1976). If food concentration was varied, the K_1 obtained at higher food concentrations was used. Omori (1979) measured growth for several stages of *Sergestes* fed on a mixed diet of *Artemia* and rotifers, whereas feeding rates were measured using pure diets. As feeding rates on *Artemia* were higher, only K_1 values calculated using the *Artemia* data were used. For the six carnivores in Table 2, estimates of ϵ range from 0.10 to 0.33, with a mean of 0.21.

The data in Table 2 suggest that the size-conversion efficiency varies no more and possibly less than the efficiency K_1. Although regression analysis of log K_1 against log W_j/W_i does not indicate a statistically significant relationship between K_1

TABLE 2. Predator–prey size ratios (W_j/W_i), conversion efficiencies (K_1), and particle-size conversion efficiencies (ϵ) obtained from published data on carnivorously feeding zooplankton. Body size is given in dry weight or weight of carbon (C). The mean and coefficient of variation (standard deviation/mean) is shown for ϵ and log K_1.

Predator (size, W_j)	Prey (W_i)	W_j/W_i	K_1	ϵ	Reference
Clione limacina (3.01 mg)	*Spiratella retroversa* (0.188 mg)	16	0.61	0.18	Conover and Lalli (1974)
Calliopus laeviusculus (~1.5 mg C)	*Calanus* spp. (90 μg C)	17	0.39	0.33	Dagg (1976)
Sagitta hispida (145 μg)	*Artemia* (1.77 μg)	82	0.34	0.24	Reeve (1970)
Sergestes similis	*Artemia*				
PL1 (130 μg C)	(0.76 μg C)	170	0.31	0.23	Omori (1979)
PL2 (220 μg C)		290	0.37	0.18	
PL3 (380 μg C)		500	0.21	0.25	
PL4 (550 μg C)		720	0.22	0.23	
Calanus helgolandicus	*Eliminius modestus*	534	0.52	0.10	Corner et al. (1976)
Euphausia pacifica (2.32 mg C)	*Artemia* (0.55 μg C)	4200	0.26	0.16	Lasker (1966)
			—	0.21	mean
			—	0.31	SD/mean
			0.34	—	logarithmic mean of K_1
			0.33	—	SD/mean for log K_1

and W_j/W_i, the coefficient of variation for ϵ (Table 2) is less than that for log K_1, indicating that the size-conversion efficiency is at least as uniform as K_1. Hence, in an ecological model, it would appear to be just as valid to assume a constant ϵ as to assume a constant K_1.

Reliable estimates of size-conversion efficiency for pelagic fish from published data are difficult to make. Much of the work on fish-conversion efficiencies has been summarized by Brett and Groves (1979), who obtained an average K_1 of 0.29 from the published data on laboratory experiments in which rations were well above maintenance levels. Unfortunately, predator–prey size ratios are not usually available simultaneously, especially because many studies involve feeding of fish on artificial diets. One useful study provides simultaneous information on both K_1 and predator–prey ratios of walleye (*Stizostedion vitreum vitreum*) under natural conditions. Swenson and Smith (1973) estimated the food consumption of walleye in Lake of the Woods, Minnesota, from stomach contents and a knowledge of digestion rates. From growth rates they then calculated conversion efficiencies averaging 20%. Because both number and weight of fish consumed by walleye are given, a predator–prey size ratio can be calculated. This averages 2.1×10^3, giving a size-conversion efficiency of $\epsilon = 0.21$, which is the same as the average calculated for the invertebrates in Table 2.

Although both K_1 and the predator–prey size ratio appear in the equation for the size-conversion efficiency (equation 5), these parameters are not necessarily independent of one another. Paloheimo and Dickie (1966) suggested that consumption of larger food organisms may result in a higher conversion efficiency and that this might be related to grazing efficiency. Kerr (1971), after considering the energy requirements of searching for prey, concluded that growth efficiency decreases with decreasing size of prey, relative to the predator size. Confer and Blades (1975) concluded that the consumption of larger and more visible carnivorous zooplankton by pumpkinseeds more than compensates for the energy lost by the addition of another trophic level. These studies suggest that a compensatory mechanism exists such that changes in predator–prey size ratios will result in less than expected changes in the size-conversion efficiency ϵ. In fact, lake trout (*Salvelinus namaycush*) production in several Ontario lakes appears to be proportional to primary productivity, irrespective of the number of trophic levels involved, indicating that the food resource is utilized less efficiently in shorter food chains (Kerr and Martin 1970). Hence, size-conversion efficiency may be relatively more constant than the conversion efficiency K_1, a possibility already suggested by the data in Table 2. It appears, therefore, that while several models used in studying the biomass-size spectrum in pelagic systems assume a constant predator–prey size ratio and/or constant K_1 (Kerr 1974; Sheldon et al. 1977), it may be more appropriate to assume a constant size-conversion efficiency.

One estimate of size-conversion efficiency averaged over an entire ecosystem is available. Sheldon et al. (1972, 1977) observed that over a wide range of particle sizes, biomasses over equal size intervals were approximately equal, and they discuss the mechanisms which could be responsible. Using their observations in the size-corrected biomass context, this implies that as B_i (equation 13) is constant, ϵ must equal n. Sheldon et al. (1977) calculated a value for n of 0.24 using data for plankton and fish. Hence, their data provide another

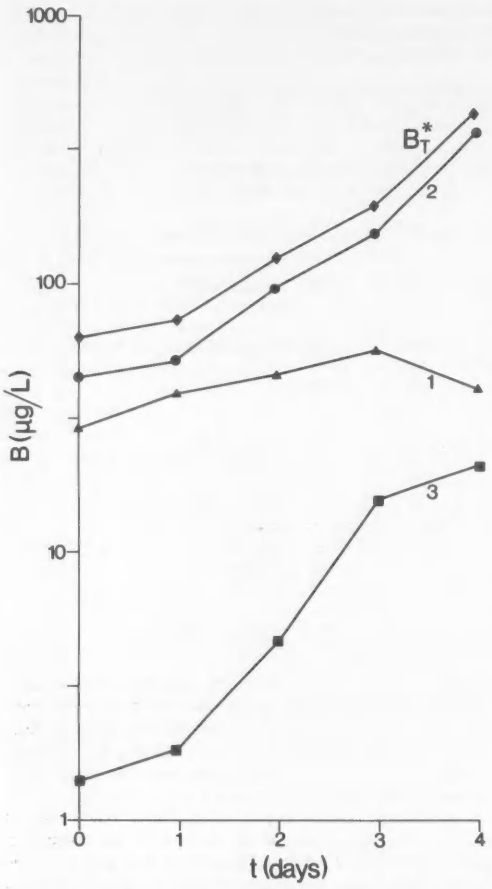

FIG. 3. Biomass in $\mu g \cdot L^{-1}$ (ash-free dry weight) of herbivorous rotifers (1), carnivorous rotifers (2), and copepods (3) in 10 L of 102-µm filtered water after 0–4 d incubation at 20°C. The total size-corrected biomass (B_T^*) in units of $\mu g^{1.21} \cdot L^{-1}$ is also shown.

estimate of ϵ (i.e. $\epsilon = 0.24$), this time using field data on the entire biomass-size spectrum. Their estimate is, in fact, reasonably close to the average value (0.21) obtained above. The small discrepancy might be due to errors caused by assuming nonpredation mortality to be negligible.

Application of the Size-Corrected Biomass Concept

An example utilizing the size-corrected biomass concept for analysis of experimental data can now be given. We used this approach to estimate production of the smaller copepods and rotifers in the Burlington Canal which connects Hamilton Bay with Lake Ontario. We collected 50 L of surface water, filtered this through 102-µm nylon screens to remove the larger organisms, divided the water into five 10-L polypropylene containers, and incubated at 20°C (approximately equivalent to Hamilton Bay surface-water temperatures in summer) for up to 4 d. Each day we filtered the contents of one container through a series of graded nylon screens and counted all copepods and rotifers, the only multicellular organisms present. We determined copepod sizes from the known relationship between copepod size and the filter size on which they are retained, and from ash-free dry weight determinations of samples of copepods in the larger size-classes (Borgmann et al. 1979). We estimated relative rotifer volumes from microscopic measurements of length and width for animals in each size-class, and calculated volumes of cylinders of equivalent length and width (diameter). These volume units were converted to ash-free dry weights by comparing total rotifer volume in a sample of mixed rotifer species with total ash-free dry weight obtained by filtering a subsample onto glass fiber filters, drying at 60°C, weighing, ashing at 500°C, and reweighing. We then calculated total biomass changes on a size-corrected biomass basis, using equation 6.

The results are shown in Fig. 3. The rate of change in the biomass of copepods (mainly *Cyclops vernalis*) and carnivorous rotifers (*Asplanchna* sp. and *Synchaeta* sp.) increased exponentially during the incubation period, but herbivorous rotifer (mainly *Polyarthra* sp., *Branchionus calyciflorus*, and *B. angularis*) biomass first increased, and then decreased, presumably because of predation by increasing numbers of carnivores. Because the degree of utilization (if any) of phytoplankton by each of the carnivorous species and the degree of predation of copepods on rotifers (or vice versa) are not known, it is not possible to calculate the rate of conversion of one animal species into another. However, the total size-corrected biomass can be determined, assuming an average size-conversion efficiency of $\epsilon = 0.21$, and this is also shown in Fig. 3. Units for B_T^* are $\mu g^{1+\epsilon} \cdot L^{-1}$. As carnivorous rotifers compose the largest biomass group, B_T^* changes follow carnivorous rotifer changes most closely. Regression of log B_T^* against t gives a slope of 0.47 d^{-1}, and because the initial size-corrected biomass was 64 $\mu g^{1.21} \cdot L^{-1}$, the initial rate of increase in B_T^* (i.e. dB_T^*/dt, equation 7) was 30 $\mu g^{1.21} \cdot L^{-1} \cdot d^{-1}$. The potential biomass production rate of fish feeding directly or indirectly on these zooplankton under steady-state conditions can be calculated using equation 10 and $F = 30\ \mu g^{1.21} \cdot L^{-1} \cdot d^{-1}$. Hence, this microzooplankton production represents a potential fish production of 1.02 $\mu g \cdot L^{-1} \cdot d^{-1}$ for 10 g fish (dry weight), or 0.39 $\mu g \cdot L^{-1} \cdot d^{-1}$ for 1 kg fish.

Discussion

The concepts of particle-size-conversion efficiency (ϵ) and size-corrected biomass ($B^* = BW^{\epsilon}$) can provide a rapid and easy means of analyzing data on production and standing stocks of animals in pelagic environments, without the need for specifically identifying trophic level (e.g. Fig. 3). Some of the theory discussed above is not entirely new, and in a sense represents a reformulation of ideas developed previously (e.g. Kerr 1974; Sheldon et al.1972, 1977; Platt and Denman 1977, 1978). In particular, Sheldon et al. (1977), using assumptions such as insignificant nonpredation mortality, constant K_1 and predator–prey size ratios, similar standing stocks for all particle sizes, and the existence of a

steady state over long time intervals, were able to explain the shape of the particle-size spectrum and could calculate fish production in some parts of the oceans from primary production and vice versa. The present approach differs from that of Sheldon et al., and other authors, in that the assumptions of constant K_1 and predator−prey size ratios are combined into a single assumption, a constant ϵ. This allows for variations in the predator−prey size ratio, although K_1 is assumed to vary simultaneously. As indicated above, there is some evidence to suggest that K_1 is in fact affected by predatory−prey size ratios in such a way as to reduce variations in ϵ (e.g. Paloheimo and Dickie 1966; Kerr 1971).

In addition to combining the concept of a relationship between K_1 and predator−prey size ratios with previous pelagic ecosystem models, my reformulation has two major advantages. First, production of any species, or group of species, can be defined on a size-corrected basis and is then additive with production of any other species, regardless of the trophic relationship between the two groups of animals. For example, total size-corrected zooplankton production can be defined and calculated despite the varying sizes of zooplankters, even though some are herbivores, some omnivores, and some carnivores. Potential fish production resulting from this zooplankton production can then be estimated, as related to the size of the fish (e.g. Fig. 3 and discussion thereof). Unlike the model of Sheldon et al. (1977), no relationship between organism size and growth rate need be assumed to do this, although such a relationship must be assumed if analysis of the shape of the particle-size spectrum is desired. (A relationship between growth rate and organism size was assumed above to utilize the data of Sheldon et al. to obtain an additional estimate of ϵ.) Secondly, my reformulation results in a considerable mathematical simplification over more elaborate models (e.g. Platt and Denman 1977, 1978), primarily because there is no loss in size-corrected biomass as biomass is transferred up the food chain. In fact, equations 10 and 13 are similar to the very simple, hypothetical case considered by Platt and Denman (1978) where biomass losses due to respiration and decomposition were ignored.

In the application of the size-corrected biomass concept to production measurements in individual species, several points should be mentioned. For populations which have a high reproductive rate, large offspring and little change in mean body size, the rate of increase in the size-corrected biomass is directly proportional to the rate of increase in the biomass (i.e. if $dB/dt = rB$, then $dB^*/dt = rB^*$). However, for oganisms which undergo synchronous increase in size during some phase of the life cycle, the size-corrected biomass will increase more rapidly than the biomass. For example, if $W = W_o e^{gt}$ (Borgmann et al. 1979), then because $B^* = BW^{\epsilon} = NW^{1+\epsilon}$, it follows that $dB^*/dt = (1 + \epsilon)\, gB^*$, assuming no mortality. On the other hand, during reproduction, some species may produce small offspring similar in size to the food particles consumed by adults. This results in a net loss on a size-corrected biomass basis, as B^* is determined from size rather than trophic level. On a whole community basis, this makes sense, for predators at higher trophic levels gain no benefit from production that does not increase particle size and hence keeps potential food at a size too small to be effectively utilized. When these offspring grow in size, the benefit to higher trophic levels increases more rapidly than the rate of increase in biomass alone would suggest, and hence the more rapid increase in B^*.

The size-conversion efficiency and the size-corrected biomass therefore provide a means of analyzing and comprehending an otherwise often complex system. More estimates are now needed of size-conversion efficiency under conditions as natural as possible, as well as information on factors which might influence this efficiency (e.g. degree of eutrophication, etc.). Unfortunately, many studies on conversion efficiencies (i.e. K_1), especially in fish, are done under laboratory conditions with artificial diets, and experiments on natural food selection are not usually concerned with growth efficiency.

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Effects of Drilling Muds on Behavior of the American Lobster, *Homarus americanus*, in Water Column and Substrate Exposures

JELLE ATEMA, DALE F. LEAVITT, DIANA E. BARSHAW, AND M. CARMELA CUOMO

Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, USA

ATEMA, J., D. F. LEAVITT, D. E. BARSHAW, AND M. C. CUOMO. 1982. Effects of drilling muds on behavior of the American lobster, *Homarus americanus*, in water column and substrate exposures. Can. J. Fish. Aquat. Sci. 39: 675–690.

Studies were conducted to explore the effects of drilling muds on various aspects of lobster behavior directly related to survival in the field. Toxicity of different drilling muds varied from immediately lethal to adult lobsters to apparently harmless to postlarval stages, with a variety of intermediate effects. Both the chemical toxicity in the water column and the physical effects of covering the substrate with drilling mud were studied, and both interfered with normal lobster behavior. The studies are mainly concerned with postlarval lobsters (stages IV and V), i.e. just after settling on the bottom. They were tested in 36-d chronic exposures (7 mg/L) and in seminatural aquaria with 1-mm layers of drilling mud covering the substrate. Toxicity in the water column manifested itself in feeding and molting delays, severe delays in shelter construction, increased walking and swimming, unprovoked tail flipping, and lethargy. A natural bay mud used as a control caused no such effects. Physical effects of substrate cover were apparent in experiments with 1-, 2-, and 4-mm layers of drilling mud and similar layers of a mixture of bentonite and barite covering a natural mud substrate. In depths of 4 mm both kinds of substrate cover caused severe delays in shelter construction and in quality of burrows constructed. Thus, substrates with 4-mm to perhaps as little as 1-mm covering of drilling mud may cause increased exposure of lobsters to predators and currents, resulting in the substrate becoming unsuitable for lobster settling and survival.

Key words: drilling muds, lobster, behavior, toxicity, shelter construction, molting, feeding, survival

ATEMA, J., D. F. LEAVITT, D. E. BARSHAW, AND M. C. CUOMO. 1982. Effects of drilling muds on behavior of the American lobster, *Homarus americanus*, in water column and substrate exposures. Can. J. Fish. Aquat. Sci. 39: 675–690.

Des études ont été menées dans le but de déterminer les effets des vases de forage sur divers aspects du comportement du homard, directement liés à la survie sur le terrain. La toxicité des différentes vases de forage varie : elles peuvent causer une mort immédiate de homards adultes ou être apparemment sans effet sur des stades postlarvaires, une variété d'effets intermédiaires étant comprise entre ces extrêmes. Nous avons étudié à la fois la toxicité chimique dans la colonne d'eau et les effets physiques d'une couche de vase de forage sur le substrat. L'un et l'autre entravent le comportement normal du homard. Les études ont porté surtout sur les stades postlarvaires (IV et V), c.-à-d. juste après descente au fond. Les organismes furent soumis à des expositions chroniques (7 mg/L) de 36 d, d'une part, et testés dans des aquariums semi-naturels avec substrat recouvert de couches de 1 mm de vase de forage, d'autre part. La toxicité dans la colonne d'eau se manifeste par des retards dans l'alimentation et la mue, de sérieux retards dans la construction des abris, une activité de marche et de nage accrue, des coups de queue non provoqués et léthargie. Il n'y a pas d'effets de ce genre avec de la vase de baie naturelle comme témoin. Des expériences avec des couches de 1, 2 et 4 mm de vase de forage sur le substrat et couches semblables d'un mélange de bentonite et de barite sur un substrat de vase naturelle montrent des effets physiques d'une telle couverture. Une couche de 4 mm des deux matériaux cause de sérieux retards dans la construction des abris et influe sur la qualité des tunnels construits. C'est dire que des substrats recouverts d'une couche de vase de forage comprise entre 4 et aussi peu que 1 mm peuvent résulter en une exposition accrue des homards aux prédateurs et courants et rendre ce substrat impropre à leur établissement et à leur survie.

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OFFSHORE drilling for oil and gas along the North Atlantic coast of the American continent may bring about environmental changes that could affect the rich fishing grounds in the area, particularly George's Bank and the submarine canyon heads immediately south. The discharge of drilling muds during drilling, for example, 2854 barrels per hole in 85 d (Meek and Ray 1980), is one aspect of the environmental consequences of drilling. Hydrographic studies (Bothner et al. 1981) have shown that the sedimentation sinks southwest of the Bank, termed the "mud patch," are likely areas of drilling mud deposition from George's Bank drilling operations.

Drilling muds are used to cool rotating bits, to carry rock cuttings to the surface, to lubricate drilling strings, and to act as plaster to prevent the drilled rock formation from collapsing. Their multiple functions are reflected in the varying and complex compositions of additives, which include bactericides, corrosion inhibitors, emulsifiers, lubricants, surface-active agents, thinners, and dispersants, depending on such factors as well depth, substrate drilled, and temperature (Land 1974; Wright 1975).

Drilling muds may contain chemicals known to be toxic to estuarine and marine organisms (Cantelmo and Rao 1978; Cantelmo et al. 1978; Conklin and Rao 1978; IMCO 1978; Rao et al. 1978). Diesel oils are some of the many fractions of petroleum hydrocarbons included in drilling mud which show toxic effects to marine organisms in amounts as little as 0.3 mg/L (Atema 1976; Capuzzo and Lancaster 1981). Tagatz et al. (1978) showed that a 2-mm layer of drilling mud could significantly alter the macrobenthic community in an estuarine environment. Many years of drilling in the Gulf of Mexico resulted in studies on toxic effects of drilling muds on warmwater organisms (Rao 1978; Tagatz et al. 1978), but there has been little research on cold-water species. Apart from chemically toxic effects, drilling muds may exert physical effects. These have, thus far, not been studied explicitly.

With a few exceptions (Rao et al. 1978; Fox and Rao 1978) most toxicity studies on drilling muds have been limited to LC_{50} tests, establishing lethal concentrations of drilling muds (Daugherty 1951; Cabrera 1971; Chesser and McKenzie 1975; Sprague and Logan 1979). Laboratory animals, however, have been seriously affected in many ways by sublethal exposures to pollutants (McIntyre and Pearce 1980; Capuzzo 1981). In the open sea, they may not be able to compete successfully for food, shelter, or mates, and may become easy victims of predation. Behavioral tests can investigate such sublethal effects (Atema 1976; Olla et al. 1980). Such studies require a solid baseline of behavioral and ecological research on the tested organism before one can realistically interpret experimental results (Olla et al. 1980). Sublethal effects have been shown in various organisms exposed to drilling mud components (Cantelmo et al. 1978; Tagatz et al. 1977, 1978).

With these considerations in mind and assuming that the major biological effects of drilling mud dispersal will be felt in the benthic coastal community, we chose the American lobster (*Homarus americanus*) to test the effects of drilling muds in Northwest Atlantic waters. This animal is found extensively along the Atlantic coast, including the George's Bank area and in the canyon heads south of the Bank (Cooper and Uzmann 1980). During the fourth larval stage this animal leaves the water column and becomes entirely benthic, relying solely on the substrate for food and shelter.

After initial toxicity tests were performed on adult lobsters, early postlarval lobsters were chosen for the bulk of this study as these are the first benthic stages. In a number of marine organisms, the young stages have proven to be more sensitive than adults (Decoursey and Vernberg 1972). Also, molting is most frequent at these young stages and the molting process is by itself a cause of stress and vulnerability for lobsters (Atema and Cobb 1980). It has been shown that just after molting, when the shell is relatively permeable, grass shrimp are particularly sensitive to toxic substances (Conklin and Rao 1978). The postlarvae and very young juveniles are so shelter bound that they are rarely discovered in the field. In the laboratory, postlarval lobsters establish shelters (i.e. dig burrows or find suitable crevices) soon after settling on the substrate and exhibit a preference for certain types of substrate on which to settle (Cobb 1971; Berrill and Stewart 1973; Howard and Bennett 1979; Botero and Atema 1982). When a suitable substrate is not available, settling is delayed (Templeman 1936; Botero and Atema 1982).

In this study, long-term effects of drilling muds in water on the feeding and molting of postlarval lobsters were measured over 36 d of constant exposure in a flow-through system, while physical and chemical effects of a single dose of drilling mud on shelter behavior were measured in a seminatural situation. The dosing level (up to 10 mg/L flow through) was chosen as such levels have been calculated to occur 1 km down current from an actual discharge using barium as an indicator for drilling mud concentration (Gettelson and Laird 1980). In seminatural aquaria, we were interested in the effects of thin layers (1−4 mm) of drilling mud covering the natural substrate. Such sedimentation can be expected to occur many kilometres down current from a discharge, depending on local hydrographic conditions (Meek and Ray 1980). The purpose of this study was to measure the range of toxicities of a variety of drilling muds, and to indicate both chemical (water column or substrate contact) and physical effects of drilling mud discharge on a broad range of lobster behaviors of vital importance. Alterations in postlarval behavior may affect future generations of lobsters in an exposed area, even if the effects are not readily apparent at the time of drilling and dumping.

Initial Evaluation

Using adult lobsters, we assessed the range of effects drilling muds had under laboratory conditions. The drilling muds used in these studies were "spent" muds collected from drilling rigs in the Gulf of Mexico (Mobile Bay muds, DM−X, M-16, and M-25) and from a land-based drilling operation in Florida (Jay muds, J-5 and J-7). These muds are characterized in Table 1 and were supplied by Dr Norman Richards, Environmental Protection Agency, Gulf Breeze Laboratory, Florida.

MATERIALS AND METHODS

Ten lobsters (5 male and 5 female, carapace length 57−88 mm) were placed individually in 100-L aquaria which each contained a 2.5-cm layer of sand substrate and a glazed clay shelter. They were supplied with running, air-saturated

TABLE 1. Characteristics of drilling muds used in tests on lobster behavior and survival.

Drilling mud (DM) used	Symbol	Date collected	Depth from which retrieved (m)	Density (g/mL)	Funnel viscosity (s/L)	pH	Calcium (mg/L)	Water content (%)	Diesel oil (%)	Phenol[a] (mg/L)
Unknown	DM−X	—[b]	—	—	—	—	—	—	—	—
Mobile 16	M-16[c]	June 26, 1979	4694	4.6	42	11.0	trace	—	Not tested	—
Mobile 25	M-25[c]	Sept. 4, 1979	6222	6.2	53	11.8	40	—	Not tested	—
Jay 5	J-5	July 29, 1980	4098	4.5	78	11.4	120	90	2	0.45
Jay 7	J-7	Aug. 4, 1980	4453	4.5	—	11.5	—	—	4	0.33

[a]From Derby (1981).
[b]Data not available from drilling mud source.
[c]These muds were referred to as DM-2 and DM-3, respectively, in Derby and Atema (1981). NOTE: Further characterization of drilling mud chemistry for J-5 and J-7 can be found in Derby (1981).

seawater (ambient salinity). The flow-through system, described in detail elsewhere (Atema et al. 1979), consisted of one control and one experimental head tank. The experimental head tank supplied six individual 100-L tanks. The overflow from the above tanks entered a holding tank where five additional lobsters were individually held to determine the effects of drilling mud effluent (*Effluent exposure*). The control head tank supplied four individual 100-L tanks. Individual tanks, both experimental and control, had inflows ranging from 400 to 460 mL/min. The lobsters were allowed to acclimate to laboratory conditions for at least 2 wk. They were fed pieces of mussel (*Mytilus edulis*) shortly before introduction of drilling mud, and their behavior was observed. Drilling mud was poured at one time into each experimental tank.

In the first test (Dec. 1978; water temperature 8°C), three experimental tanks received 1700 mL of drilling mud (DM−X) (*High exposure*) and three received 100 mL of DM−X (*Low exposure*). The higher volume of drilling mud was chosen to form a 10- to 12-mm layer over the sand substrate; the lower volume was chosen to reach a depth of 1−2 mm. Two control tanks received 1700 mL of natural ocean bay mud (BM), collected locally in Buzzard's Bay, MA, and two were left undistrubed (C). The lobsters were observed at morning and afternoon feedings for 4 d. The time it took each lobster to alert to the presence of food and to find the food were recorded. After 4 d of exposure, the lobsters were removed from the system and frozen for future chemical analyses.

In a subsequent test (Sept. 1979; water temperature 21°C), three experimental tanks (*High exposure*) received 1000 mL of drilling mud (M-16) instead of 1700 mL. Because no behavioral differences were observed between seawater and clean mud controls in December 1978, controls in the latter experiment were not treated with clean mud. Apart from these differences the procedures were identical.

RESULTS

The most severe effects of DM−X appeared in those lobsters exposed to the highest concentrations of drilling mud and to the drilling mud effluents.

High exposure — Only 4 h after the addition of the drilling mud, two of the three lobsters showed serious effects: one was lying on its back moving only its walking legs; the other had apparently tailflipped into a corner and was stuck standing on its head with its rostrum buried up to its eyestalks, and no obvious capability to right itself. Neither of these animals regained mobility during the experiment, but became weaker as time progressed. Even poking them provoked only the most feeble response from a few legs. The third lobster in the high-exposure group showed reduced physical coordination after 6 h and severe effects similar to the other two after 8 h. While this animal was always more active than the other two, it also weakened progressively over the 4 d. None of these three animals ate after the addition of drilling mud and initially demonstrated only weak responses to the presence of food, even when it was dropped directly on their primary chemoreceptive organs, the antennules and dactyls.

Effluent exposure — Two of the lobsters exposed to the effluent of 5400 mL of drilling mud in the holding tank died before the end of the experiment. The three other lobsters of this group showed increasing inability to coordinate movements and at the end of the experiment were comatose.

Low exposure — The lobsters exposed to low concentrations of DM−X were less affected than the heavily exposed animals. They remained active to varying degrees throughout the experiment, digging and bulldozing the substrate so that after 6 h no drilling mud was obvious as a layer on top of the sand. Compared to preexposure behavior, they appeared to be less coordinated. One obvious effect of the drilling mud exposure was the cessation of feeding activity. All three animals alerted to the presence of food, but failed to find it, either because they never searched or because, if they did touch the food, they seemed to be unaware of it. Two of these animals did recover; one was eating after 30 h, the other after 54 h from the time of addition of the drilling mud.

Controls — None of the control lobsters, neither in C nor in BM treatment, changed their behavior over the 4-d period. The BM lobsters, especially, were very active as their tanks were always turbid and they alerted to and ate the pieces of mussel fed to them.

M-16 — The next drilling mud (M-16) gave very different results. Even lobsters exposed to the 7-mm layer showed little or no effects. All animals ate normally and the only obvious

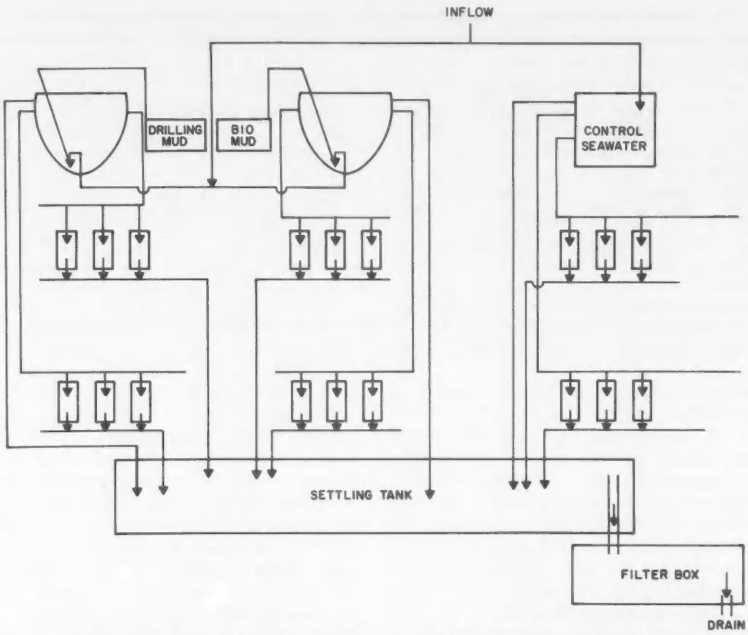

FIG. 1. Flow-through exposure system for juvenile lobsters. Each head tank (DM, BM, or C) supplies 40 trays, totalling 120 test animals. Test muds are introduced by syringe pump into the head tanks.

difference in behavior was that animals exposed to drilling mud were found more often inside their shelters.

Chronic Exposure

In a flow-through system, we investigated the long-term effects of drilling muds and clean bay mud on molting frequency, feeding behavior, and survival of postlarval lobsters. Drilling muds as described in Initial Evaluation were used.

MATERIALS AND METHODS

Stage IV lobsters, siblings, were held in kreisels (Hughes et al. 1974) and fed frozen brine shrimp (*Artemia* sp.) until used in experiments. There were three treatment groups: the first (J-5) received J-5 drilling mud; the second (BM) received clean bay mud, collected locally in Buzzard's Bay, MA, and prepared to a consistency similar to drilling mud; and the third (C) received only seawater (ambient salinity, air-saturated, temperature range 10–21°C). Both mud exposures were maintained at an approximate concentration of 10 mg/L. Each of the three treatment groups had 40 animals, held individually in previously leached plastic trays (7 × 22 × 5 cm) under a light regime of 14 h light:10 h dark. Each tray contained a small rock for shelter. Frozen brine shrimp were thawed and fed ad libitum twice daily throughout the experiment, except when measuring food intake as described below. The lobsters were maintained for 5 d, during which time any unhealthy animals were replaced.

The three groups of trays were placed in a flow-through seawater distribution system each topped by its own head tank (Fig. 1). Seawater entered the head tanks through a jet nozzle at a rate of 9.6 L/min, and the flow was divided through a manifold to supply each tray with an approximate flow of 250–300 mL/min. A V-cut overflow, covered with nylon screen, drained each tray. Both drilling mud and biological mud were injected by syringe pumps into the jet stream of water within the head tanks, thus preventing coagulation. Swirling action created by the conical shape of the head tanks and the downward motion of the jet stream kept the muds in suspension in the head tanks. The syringes were replaced three times daily and at these times the amount of mud that had entered the system was recorded. From these data the mean exposure level over 36 d was calculated: DM 7.7 ± (SE)0.4 mg/L; BM 6.7 ± 0.4 mg/L. These exposure levels are not significantly different ($P > 0.05$). Settling of suspended particles occurred in the distribution system and in the individual trays. To prevent clogging, the distribution manifold system was cleaned as necessary and, to avoid heavy substrate cover in the trays, settled debris was removed twice daily. For complete cleaning, the trays were replaced every 4 d.

Food detection and consumption were measured daily. Food detection was measured as the time (s) before a lobster alerted to the presence of one brine shrimp placed 1 cm away. "Alert" was defined as an obvious movement oriented either to the water surface or to the location of the food. "No alert" was recorded if the animal had not responded within 120 s. Each day 30 animals, 10 from each group, were tested individually. Food consumption was determined by introducing

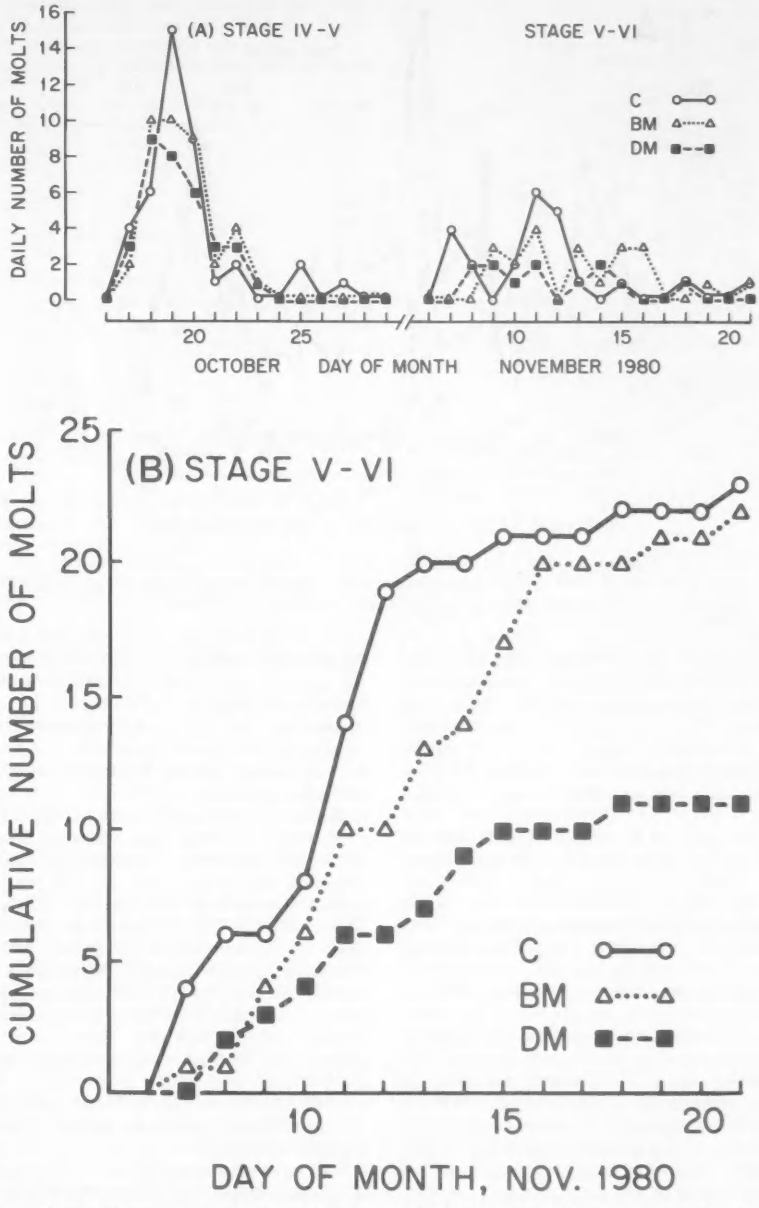

FIG. 2. (A) Daily number of animals molting (stages IV to V and V to VI). Mean temperature during first molt period 14.7°C, during second molt period 10.3°C; (B) Cumulative number of molted animals for the second molt only (stage V to VI).

five brine shrimp to each of the 30 animals used above, and, after 16 h, counting the number remaining. Each day 30 different animals were tested. This rotation resulted in all lobsters being tested at least every 4 d.

The experiment was continued for 5 wk during which the animals developed from stage IV to stage VI. Records of

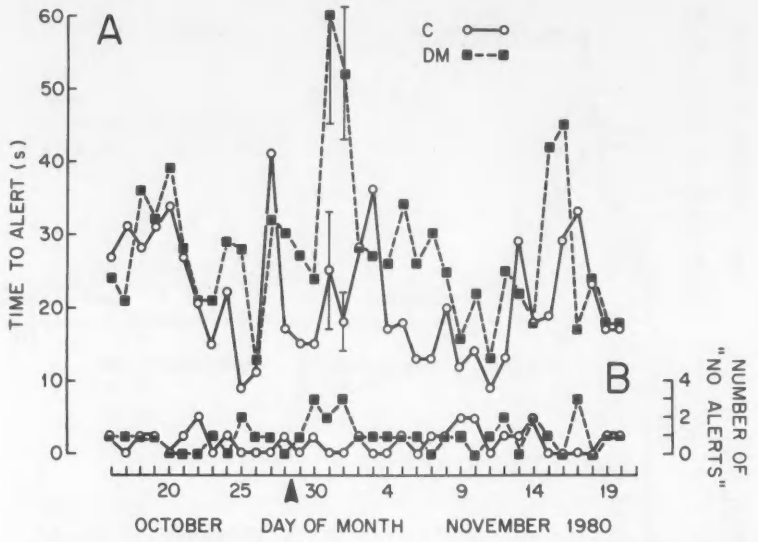

FIG. 3. (A) Mean time to alert (n = 10 animals/treatment·d^{-1}). BM similar to C and not shown for clarity. Arrow at October 28, 1980, indicates introduction of new J-5 sample. Data for October 30–31 shown with standard error bars; (B) total number of animals per day not alerting (n = 10 animals/treatment·d^{-1}). BM deleted as in 3A.

animals that had molted or died were made and the molted shells or dead carcasses saved for future chemical analyses. At the end of the experiment, all surviving lobsters were examined for damage (i.e. missing appendages), their size was determined by measuring carapace length (CL) from the postorbital margin to the posterior dorsal median point of the carapace, and the animals were frozen for future chemical analyses.

The data were evaluated for differences between treatments based on statistics in Zar (1974), Sokal and Rohlf (1969), and Grubbs (1950).

Measurements and statistical evaluations — The following data were recorded and analyzed for differences between treatments.

1) Mortality: the number of animals found dead (3 × 2 contingency table, χ^2).

2) Damage: the number of lobsters missing appendages at the end of the experiment (3 × 2 contingency table, χ^2).

3) Molting: number molted (3 × 2 contingency table, χ^2).

4) Growth: final mean carapace length (one-way ANOVA).

5) Food consumption: the mean number of *Artemia* eaten by 10 lobsters per day (Kruskal–Wallis ANOVA).

6) Time to alert: differences between treatments and between days of the experiment (two-way ANOVA).

7) No alerts: the total number of lobsters that failed to alert at least once during the experiment (Cochran's Q-test).

RESULTS

Mortality, damage, and overall appearance — No significant differences in mortality or in damage between the three treatments were found. However, when the dead and damaged groups were added there was a significantly greater number of damaged or dead lobsters in the J-5 group. Also, observations showed that J-5 lobsters in the last half of the experiment showed poor coordination and dark pigmentation in the appendages compared with the other groups. This was not further quantified.

Molting and growth — During the experiment, most lobsters molted twice, from stage IV to V and from stage V to VI. The lobsters in the three treatments all had approximately the same molt peak during the first molt (Fig. 2). In group J-5, 35 of the animals molted from stage IV to V, compared to 34 in BM and 40 in C. This difference is not significant (Table 2). Three of the nonmolting J-5 animals subsequently died before the experiment ended. Significantly more lobsters molted from stage V to VI in BM and C treatments than in J-5 treatment (22 and 23 versus 11, respectively, Table 2), although no distinct molt peak was observed. There was no difference in the final carapace lengths among treatments (Table 2).

Food consumption — There was no difference in the amount of brine shrimp eaten by the lobsters in the three treatments (Table 2).

Time to alert and no alert — J-5-exposed animals took significantly longer to alert ($P < 0.01$) than did those exposed to BM or C (Table 2). The difference was due to a change in alerting behavior during the middle third of the experiment as the first and last thirds of the experimental period, when tested separately for significance, showed no differences (Fig. 3). This period coincides with a change to a second shipment of J-5 drilling mud. There was a significant difference between the number of times the lobsters did not

TABLE 2. Effects of chronic exposure of J-5 drilling mud and natural bay mud (BM) on lobster behavior and survival. (*Statistical significance at $P < 0.05$; **statistical significance at $P < 0.01$.)

Test measurement		J-5 $n = 40$	BM $n = 40$	C $n = 40$
Mortality		8	7	4
Damage		9	4	5
Mortality and damage		17	11	9*
Number molted (stage IV−V)		35	39	40
Number molted (stage V−VI)		11**	22	23
Final size (CL, mm)	$\bar{X}$(SE)	6.2(0.1)	6.4(0.1)	6.4(0.1)
	n	31	29	36
Food intake (No. *Artemia*/10 lobsters·d^{-1})	$\bar{X}$(SE)	7.9(0.9)	9.8(1.0)	9.0(1.0)
Time to alert (s)	$\bar{X}$(SE)	26(1)**	23(1)	21(1)
	n	32	29	36
No alert		27	26	20

alert to food between the three treatments (Table 2). A sharp increase in the number of lobsters not alerting was noted for 3 d after we started to use the new sample of J-5.

Substrate Choice Tests

In seminatural aquaria, we investigated the effects of thin layers of drilling mud covering the surface of the natural substrate on postlarval lobsters.

MATERIALS AND METHODS

Stage IV to VI lobsters, kept under near natural conditions in a holding tank, were used in these experiments. The tank contained a shell rubble substrate with multiple shelters, running ambient seawater, and ambient light. The lobsters were fed frozen *Artemia* and fresh mussel ad libitum. No lobster was used more than once.

Eight hours before each trial, eight 100-L test aquaria (55 × 55 × 35 cm) (Fig. 4) were layered with 4−6 cm of intertidal mud from Hadley's Harbor, Buzzard's Bay, MA. The mud was collected within 8 h of being used. The aquaria were then filled and maintained with a constant flow of fresh, ambient seawater which drained through a central standpipe. Water depth was ~25 cm above the substrate. The flow was regulated and kept equal between the eight aquaria by fitting each individual aquarium with a small head tank having a standard water level. Water flowed from each of the head tanks through identical hoses to the four corners of each aquarium. Small rocks (2−3 cm in diameter) were placed in each corner and in the center of each quadrant as starting points for burrow construction. The aquaria then stood overnight with the seawater running to allow the mud to settle.

Three relevant situations were tested. First, does a thin layer of drilling mud interfere with a lobster's ability to establish and maintain a shelter (No-Choice)? Second, will a lobster show a preference if given a choice between a natural and a drilling mud covered substrate (Choice)? Third, after a shelter has been established on a clean substrate, does the addition of drilling mud alter lobster behavior (Disturbance)? For each experiment, three replicate runs were made to total 12 drilling mud exposed and 12 control tests. All substrate choice tests were run completely for two different drilling muds, M-16 and J-5. In addition, J-7 was also used in the Choice test.

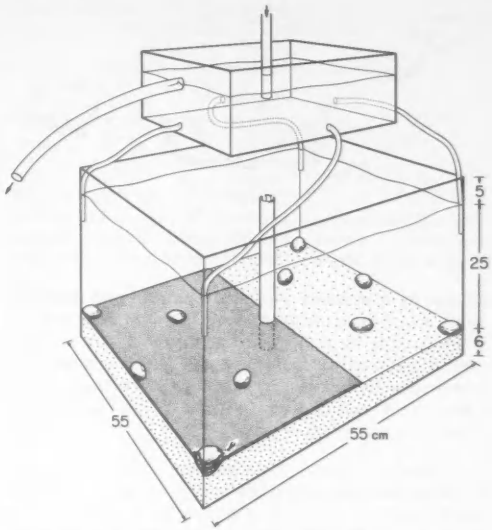

FIG. 4. A typical 100-L test aquarium used in substrate tests. Juvenile lobster outside burrow drawn to scale.

No-Choice tests — Immediately preceding the experiment, a layer of ~1 mm of drilling mud (360 mL) was carefully spread over the entire surface of the mud substrate in four of the eight aquaria; the other four served as controls and received no additional mud layering. When the water in the tanks was sufficiently clear for behavioral observations, eight healthy lobsters were captured from the holding tank and one lobster was dropped into each aquarium. Behavior and position of the animal and burrow site were recorded on a strict time schedule. For the 1st half hour, observations were recorded every minute; for the following 2.5 h, once every 5 min; and for the next 5 h, once every 30 min. After ~24 h, one last observation was recorded, the animal's burrow was sketched, and the burrow's dimensions were measured. Recordings were made of (1) location of the animal in the aquarium, (2) activity (walking, swimming, or standing still), (3) burrowing activity (pleopod fanning, bulldozing, or digging), (4) shape and size of the burrow, and (5) number of tailflip escape responses as well as other behaviors. The animals were then removed, the mud was discarded, and the aquaria were cleaned and prepared for the next run.

Choice tests — The choice test was performed using the same basic procedure as the No-Choice test. However, instead of covering the entire substrate surface with drilling mud, only one-half of the surface was covered with a 1-mm layer (180 mL per $\frac{1}{2}$ aquarium). This was accomplished by

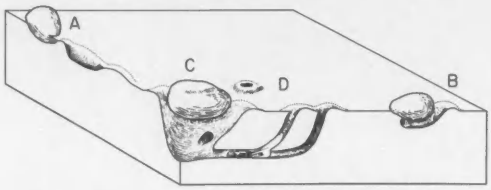

FIG. 5. Shelter quality. A, Depression; B, single opening burrow; C, two opening U-shaped burrow; D, multiple openings (here 5) of complex burrow. Juvenile lobster in burrow drawn to scale.

plished by temporarily placing a Plexiglas wall perpendicularly across the center of the tank, thus protecting one side, while layering the drilling mud on the other. After an hour, when the drilling mud had settled out of the water column, the experiment started when we dropped the lobster in. Observations were made as described above. Control tanks were as in the No-Choice tests.

Disturbance tests — Lobsters were allowed to establish residence in the aquarium before drilling mud or additional control mud was added. After introducing the lobster into the aquarium, observations were made following the same schedule as before, until all the animals had constructed a residence (burrow or depression). One hour after the last animal had established its residence, four of the aquaria had 180 mL of drilling mud layered over the side of the tank having the residence, using the same layering procedure as in the Choice test. In the four control aquaria, an equal amount of Buzzard's Bay mud (BM) was layered similarly. The control mud was prepared to resemble drilling mud in density and consistency. Observations were resumed on the same schedule as before, starting with one $\frac{1}{2}$ h of 1-min observations.

Measurements and statistical evaluations — The following behaviors were recorded and analyzed for differences between treatments.

1) Preburrowing activity: following introduction of the test animal, total activity was measured as the percent time the animal was active (walking or swimming) in the initial 30 min, or until burrowing behavior was observed (arc sine transformation, Student's *t*-test).

2) Tailflip: tailflipping is an escape response forcefully propelling the animal backwards. It was observed in these tests without apparent cause. The number of animals showing such "spontaneous" tailflips was recorded for 30 min following introduction of the lobster into the tank (2×2 contingency table, χ^2).

3) Time to bulldoze at homesite: the time (min) before an animal initiated burrowing activity at the site where the lobster's burrow was eventually located (Student's *t*-test).

4) Burrowing activity: after initiation of burrowing at the homesite, 12 observations were analyzed for lobster burrowing activity, and also, because different burrowing behaviors are used to manipulate different substrates, for type of burrowing behavior. (A) Total activity was measured as the number of observations where the animal was seen burrowing with any of three behaviors: digging, bulldozing, or pleopod fanning (Student's *t*-test). (B) Type of burrowing behavior was measured as the percent digging and bulldozing in burrowing observations (arc sine transformation, Student's *t*-test).

5) Burrow quality: burrows were categorized as complex, 2-opening, 1-opening, depression or no burrow (Fig. 5). Differences between treatments in frequency of burrow types were tested (2×5 contingency table, χ^2). Subsequently, a burrow was judged either good or poor in relation to the amount of protection offered from potential predators (2×2 contingency table, χ^2).

6) Burrow stability: the number of animals changing the site of their home burrow during the 24-h observation period (2×2 contingency table, χ^2).

For Choice tests these additional observations were made:

7) Time spent clean vs. DM: the percentage of time (min) spent on the clean substrate, compared to the DM substrate, in 30 min following introduction of the lobster (arc sine transformation, Student's *t*-test).

8) Side chosen for burrow: the side chosen (DM or Clean) was recorded and the frequencies were compared to an expected frequency of 50% per side (χ^2).

For disturbance tests these additional observations were made:

9) Initial evacuations: after being disturbed with mud, animals temporarily or permanently leaving their previously constructed burrows were enumerated. BM and DM treatments were compared (2×2 contingency table, χ^2).

10) Permanent evacuations: the number of animals permanently leaving their homesites and building new burrows after disturbance (BM−DM comparison, 2×2 contingency table, χ^2).

11) Time spent on disturbed side: the percent time (min) spent on the disturbed side (BM−DM comparison, arc sine transformation, Student's *t*-test).

12) Time until bulldozing at homesite: the time until first bulldozing observed in the predisturbed animals was used as a control for comparison with the time until first bulldozing was observed after BM or DM disturbance (one-way ANOVA, Scheffe's Multiple Contrast Test; except for J-5, where a Student's *t*-test was used because no lobsters reburrowed following the BM disturbance, leaving only two means to compare).

RESULTS

No-Choice — Differences between drilling mud and control treatments were significant in three of the nine measurements (Table 3). Spontaneous tailflip escape responses were observed only in both DM treatments. Preburrowing activity, i.e. both swimming and walking, was 98% in J-5 and 87% in C. Nearly all of this was walking for both J-5 and C treatments. Lobsters in J-5 took 91 min to begin burrowing at the homesite versus 27 min for lobsters in C. Taken together, these results indicate that on a substrate covered with 1 mm of DM, lobsters walked around incessantly, made unprovoked tailflips, and did not find a suitable burrowing place until 1 h after the control lobsters. However, they used the same burrowing techniques, constructed equally good shelters, and remained attached to these shelters as frequently as control lobsters.

Choice — When presented with a choice of substrates,

TABLE 3. Effects of M-16 and J-5 drilling muds on lobster behavior in No-Choice substrate tests. (*Statistical significance at $P < 0.05$; **statistical significance at $P < 0.01$; ***statistical significance at $P < 0.005$.)

			M-16		J-5	
Test measurement		Treatment	$\bar{X}$(SE) or no.	n	$\bar{X}$(SE) or no.	n
Preburrowing activity	a) Total activity (%)	C	65(10)	11	87(4)**	12
		DM	79(7)	12	98(1)	12
	b) Walk (%)	C	83(9)	11	100(0)	12
		DM	79(8)	12	98(1)	12
Tailflip		C	0***	11	0*	12
		DM	7	12	4	12
Time until bulldoze at homesite (min)		C	19(5)	10	27(8)***	10
		DM	52(15)	12	91(12)	10
Burrowing activity	a) Total (No. of observations)	C	9(1)	11	8(1)	11
		DM	8(1)	12	7(1)	11
	b) Bulldoze (%)	C	86(4)	11	76(6)	11
		DM	92(4)	12	72(6)	11
Burrow quality	a) Complex	C	3	7	5	12
		DM	2	10	5	12
	2-open	C	4		6	
		DM	4		5	
	1-open	C	0		1	
		DM	2		2	
	Depression	C	0		0	
		DM	2		0	
	None	C	0		0	
		DM	0		0	
	b) Good	C	11	11	11	12
		DM	10	12	12	12
	Poor	C	0		1	
		DM	2		0	
Burrow attachment		C	4	11	2	12
		DM	4	12	1	12

significant differences were observed in two of the nine measurements (Table 4). Lobsters on substrates half-covered with J-5 took two to three times as long to start burrowing for a home shelter (53 versus 20 min). In the aquaria half layered with M-16, 10 of 12 lobsters chose the side without drilling mud in which to burrow; in control tanks the choice was random. However, there was no difference in the amount of time spent walking on the DM side and the clean side of the tank. There was also no difference between DM and C treatments in the number of animals tailflipping, in burrowing activity and techniques, in burrow quality, or in burrow attachment.

Disturbance — Drilling mud had profound effects on lobsters in established burrows (Table 5). Of 12 lobsters in established shelters receiving a plume of M-16 drilling mud discharge, 11 evacuated their shelter compared to 4 lobsters receiving a similar plume of bay mud (BM). Ten of these 11 animals did not return to their original shelter and built a new one; 2 of the 4 lobsters evacuating after bay mud dumping returned to their original shelters. Those lobsters that constructed new shelters took about three times as long to find a place for its construction the second time (71 min in BM and 57 min in DM) as they had for their original shelters (22 min). The two control lobsters (BM) that did evacuate permanently took as long as the 10 DM lobsters to find a new construction site. Tailflips were observed only in DM-exposed animals. J-5 drilling mud caused four animals to evacuate their shelters versus none in BM controls. This group of four took almost nine times as long to find a homesite (105 min) as it took the entire group of 24 lobsters to do originally (12 min). There were no significant differences in the amount of time spent by evacuated lobsters on DM versus BM substrates, or in the sides chosen to build a postevacuation shelter. There were no differences in burrowing activity and techniques, in burrow quality, or in burrow attachment.

Combined tests — Five common measurements can be

TABLE 4. Effects of M-16, J-5, and J-7 drilling muds on lobster behavior in Choice substrate tests. (**Statistical significance at $P < 0.01$.)

Test measurement		Treatment	M-16 $\bar{X}$(SE) or no.	M-16 n	J-5 $\bar{X}$(SE) or no.	J-5 n	J-7 $\bar{X}$(SE) or no.	J-7 n
Time spent clean vs. DM (%)		Clean	52(9)	12	46(5)	12	53(7)	12
		DM	48(9)		54(5)		48(7)	
Tailflip		C	1	11	1	12	0	12
		DM	0	12	2	12	2	12
Time until bulldoze at homesite (min)		C	19(4)	10	20(5)**	12	51(15)	12
		DM	26(3)	11	53(11)	12	61(15)	11
Side chosen for burrow		C	10**	12	6	12	9	12
		DM	2		6		3	
Burrowing activity	a) Total (no. of observations)	C	9(1)	11	9(1)	12	6(1)	12
		DM	8(1)	11	8(1)	12	6(1)	11
	b) Bulldoze (%)	C	80(6)	11	82(6)	12	88(5)	12
		DM	80(5)	11	72(8)	12	84(3)	11
Burrow	a) Complex	C	3	11	3	12	6	12
		DM	5	12	3	12	6	12
	2-open	C	5		9		6	
		DM	2		6		6	
	1-open	C	1		0		0	
		DM	1		2		0	
	Depression	C	2		0		0	
		DM	4		1		0	
	None	C	0		0		0	
		DM	0		0		0	
	b) Good	C	8	11	12	12	12	12
		DM	7	12	11	12	12	12
	Poor	C	3		0		0	
		DM	5		1		0	
Burrow attachment		C	0	11	3	12	3	12
		DM	0	12	1	12	0	12

combined across the three types of substrate tests and different drilling muds used (Table 6). Two of these tests show highly significant differences ($P < 0.001$): spontaneous tailflipping was seen in 29 DM-exposed animals and in three controls, the time to begin home shelter construction was more than double in DM (59 min) compared with C (23 min).

Substrate Depth Tests

Apart from chemically toxic effects, drilling muds may exert purely physical effects. This was investigated, again with postlarval lobsters.

MATERIALS AND METHODS

Lobsters (stages V and VI) were obtained from the semi-naturalistic holding tank described earlier. The drilling mud used in these experiments was M-25 (Table 1). The bentonite and barite, obtained from the Gulf Breeze Laboratory, were mixed according to the established formula of 4 parts barite to 5 parts bentonite (IMCO 1978). Appropriate amounts were weighed and mixed with water to equal M-25 in density.

Eight 2-L glass beakers were filled with 8 cm of bay mud. Two rocks were placed opposite each other near the glass sides of the beaker to facilitate observations of burrow construction. A flow-through system delivered ambient seawater to all eight chambers at an equal rate of 65 mL/min. In the first of these experiments, drilling mud was evenly layered over the bay mud substrate in four of the beakers, with three treatment depths of 1, 2, and 4 mm. Only one depth was layered during each trial; there were three replicates for each treatment, totalling 12 experimental runs at each depth and a matched number of controls. In the second series of experiments, 4 mm of either drilling mud (M-25) or bentonite–barite mixture (BB) was layered over the bay mud substrate in four of the eight beakers. The remaining four beakers served as controls. Three replicates of each treatment were run for a total of 12 animals per treatment and a matched

TABLE 5. Effects of M-16 and J-5 drilling muds on lobster behavior in disturbance substrate tests. (*Statistical significance at $P < 0.05$; ***statistical significance at $P < 0.005$.)

Test measurement		Treatment	M-16 $\bar{X}$(SE) or no.	M-16 n	J-5 $\bar{X}$(SE) or no.	J-5 n
Initial evacuations		BM	4***	12	0*	12
		DM	11	12	4	12
Permanent evacuations		BM	2***	12	0	12
		DM	10	12	2	12
Time spent on disturbed side		BM	56(8)	11	61(12)	4
		DM	44(8)	11	39(12)	4
Tailflip		BM	0***	12	1	12
		DM	9	12	5	12
Time until bulldoze at homesite (min)		C[a]	22(5)[b]	22	12(2)***	22
		BM	71(26)	4	—	0
		DM	57(12)	10	106(25)	4
Side chosen for burrow (evacuated animals only)	Clean	BM	1	2	0	0
	Disturbed	BM	1		0	
	Clean	DM	9	10	1	2
	Disturbed	DM	1		1	
Burrowing activity	a) Total (no. of observations)	BM	5(1)	10	4(1)	12
		DM	8(1)	11	4(1)	12
	b) Bulldoze (%)	BM	60(5)	10	67(11)	12
		DM	77(10)	11	73(11)	11
Burrow quality	a) Complex	BM	—	—	8	12
		DM	—	—	8	12
	2 open	BM	—		2	
		DM	—		4	
	1 open	BM	—		2	
		DM	—		0	
	Depression	BM	—		0	
		DM	—		0	
	None	BM	—		0	
		DM	—		0	
	b) Good	BM	12	12	12	12
		DM	12	12	12	12
	Poor	BM	0		0	
		DM	0		0	
Burrow attachment		BM	2	12	0	12
		DM	6	12	1	12

[a]C represents time for all animals before disturbance, BM and DM represent those animals in each treatment which evacuated after the disturbance.

[b]C significantly different from both M-16 and BM, $P < 0.05$.

number of controls. The test mud was added to the beaker, and after a 20-min settling period the water column was clear. At that time, one lobster was placed into each beaker. A piece of cheesecloth over the top prevented escape.

For all experiments, observations were made every minute for the 1st half hour, every 5 min for the next 2.5 h, and every 30 min for the next 3 h. Bulldozing, digging, pleopod fanning, walking, swimming, sitting, location in beaker, and general level of activity were recorded. At the end of the first 6 h of observation, the chambers were covered with a sheet of black plastic and all lights turned off. A final observation was made at the conclusion of the 24-h experimental period. The animals were removed and measured and the burrows were measured and sketched at the end of the experiment.

For each treatment, differences between experimental and control groups were analyzed for the time until first bulldoze at homesite (one-way ANOVA, Scheffe's Multiple Contrast Test), and for burrow quality (2×2 contingency table, χ^2).

TABLE 6. Combined effects of drilling muds in 1-mm substrate layers on lobster behavior. (***Statistical significance at $P < 0.005$).

Test measurement		Treatment	$\bar{X}$(SE) or no.	n
Tailflip		C	3***	83
		DM	29	84
Time until bulldoze at homesite (min)		C	23(3)***	98
		DM	59(6)	70
Burrowing activity	a) Total (no. of observations)	C	7(1)	79
		DM	7(1)	80
	b) Bulldoze (%)	C	77(3)	78
		DM	71(3)	80
Burrow attachment		C	13	82
		DM	14	84

TABLE 7. Effects of varying depths of M-25 drilling mud on lobster behavior. (*Different superscripts indicate statistically significant differences ($P < 0.05$).)

		Depth of drilling mud layer			
Test measurement		Control $\bar{X}$(SE) or no.	1 mm $\bar{X}$(SE) or no.	2 mm $\bar{X}$(SE) or no.	4 mm $\bar{X}$(SE) or no.
Preburrowing activity	a) Total activity (%)	68(15)[a]* n=36	39(21)[a] n=12	75(27)[a] n=12	71(26)[a] n=12
	b) Walk (%)	92(20)[b]	85(37)[b]	84(30)[b]	79(28)[b]
Time until bulldoze at homesite (min)		38(15)[c] n=35	125(51)[d] n=12	103(41)[d] n=11	520(168)[c] n=8
Burrowing activity	a) Total (no. of obs.)	6(2)[f] n=35	4(2)[f] n=12	5(3)[f] n=11	2(1)[f] n=8
	b) Bulldoze (%)	86(19)[g]	90(35)[g]	92(37)[g]	79(35)[g]
Burrow	a) Complex	10[h]	0[h]	1[h,i]	0[i]
	2-open	22	11	7	3
	1-open	3	1	2	3
	Depression	0	0	1	4
	None	1	0	0	0
	b) Good	35[j]	12[j]	10[j]	4[k]
	Poor	1	0	1	8

RESULTS

With increasing substrate cover depth, the lobsters required increasing amounts of time to start bulldozing a homesite, and made progressively poorer shelters. Significant differences appeared in three of the seven measurements (Table 7). Control animals started bulldozing after 38 min, whereas a covering layer of 1 or 2 mm DM resulted in an extra hour or more before bulldozing began, and with a 4-mm layer those lobsters that did dig a homesite did not start construction until about 9 h later. One-third of the animals in this treatment (4-mm depth) did not make any burrow, and another third made only a roofless depression. In contrast, only 1 of 36 control animals did not burrow and all others constructed a good shelter with at least one opening. In 1 and 2 mm DM, generally good shelters were built. Yet in 2 mm, overall burrow quality was intermediate between controls and 4-mm treatments. Burrow quality differences were highly significant.

TABLE 8. Effects of a 4-mm layer of M-25 drilling mud or a barite–bentonite mixture on lobster behavior. (*Different superscripts indicate statistically significant differences ($P < 0.05$).)

Test measurement		Control $\bar{X}$(SE) or no.	M-25 $\bar{X}$(SE) or no.	B–B $\bar{X}$(SE) or no.
Preburrowing activity	a) Total activity (%)	74(16)[a]** $n=36$	53(18)[b] $n=12$	56(20)[b] $n=12$
	b) Walk (%)	97(20)[c]	92(27)[c]	93(27)[c]
Time until bulldoze at homesite (min)		84(19)[d] $n=24$	459(173)[e] $n=8$	700(194)[e] $n=9$
Burrowing activity	a) Total (no. of obs.)	6(1)[f] $n=24$	5(2)[f] $n=8$	2(1)[f] $n=9$
	b) Bulldoze (%)	83(19)[g]	88(32)[g]	65(35)[g]
Burrow	a) Complex	0[h]	0[i]	0[i]
	2-open	18	3	2
	1-open	3	1	2
	Depression	3	4	5
	None	0	4	3
	b) Good	21[j]	4[k]	4[k]
	Poor	3	8	8

These same effects were seen again in tests with 4-mm covering layers of either DM or BB (Table 8). In addition, in these tests, the amount of preburrowing activity (swimming and walking) was less than in controls. There were no differences between M-25 and BB treatments. Behavioral observations, however, showed that lobsters after 24 h in the DM treatment were lethargic and easily caught, offering little resistance and few escape attempts; whereas, the BB animals were as alert as controls. These observations were not quantified.

Taken together, these results show that 1- and 2-mm layers of DM covering the substrate delay digging for a shelter and slightly affect shelter quality. A layer of 4 mm DM causes serious problems in shelter construction: part of the population does not build a shelter at all, another part builds only a roofless depression, and only one-third builds a good shelter with one or two openings. Shelter construction, however, starts 9 h late. Instead of going into the substrate in about an hour, these animals are quite lethargic, spending most of the time sitting on a rock. A 4-mm layer of BB causes the same effects, but without the lethargy, making it very plausible that physical effects of a drilling mud layer alone can be detrimental to the shelter behavior of postlarval lobsters.

DISCUSSION

The drilling muds tested in these experiments showed toxicities ranging from lethal within hours for adult lobsters to apparently harmless, using our testing conditions, with a continuum of sublethal effects in between. Adults exposed to the effluent of a one-time dumping of 5.4 L of drilling mud (DM–X) in a constant flow of 2.6 L/min fresh seawater either died or became comatose within a 4-d period. Such water column effects indicate the likelihood of chemical toxicity. These effects may be distinguished from physical effects caused by suspended particles in the water column or by substrate covering: a 4-mm layer appears impenetrable for most settling and postsettling lobster juveniles. The three effects may be additive at discharge sites as shown in the experiments with postlarval lobsters, indicating that both substrate cover and water column toxicity must be considered to estimate the effects of drilling mud discharge in the marine environment.

Water column effects, as studied in the 36-d chronic exposure experiments, occurred in drilling mud (J-5) exposed animals which showed both a molt delay and interference with the process of molting, resulting in excessive loss of limbs. A total of 35% of the surviving lobsters had lost a mean of three walking legs (range 2–5). Although these lobsters with missing appendages were technically alive, they were ecologically dead, i.e. we must assume they would be easy prey in the field. Mortality and damage combined were significantly greater in J-5 than in the two control groups. Water column effects also manifested themselves in feeding interference: when a new sample of J-5 was introduced in the flow-through system a significant number of animals did not react to the presence of food, and others showed significant delays in alerting to it. These behavioral effects may be related to the changes in response to food odors observed earlier in lobster chemoreceptors which had been exposed briefly to 10 and 100 mg/L of drilling muds (Derby and Atema 1981; in that paper M-16 and M-25 are referred to as DM-2 and DM-3, respectively). At the population level, the probable consequences of such interference are clear. Mortality and damage

reduce the DM-exposed population of juvenile lobsters, and delays in or the absence of feeding behavior may reduce their competitiveness against others and will reduce their growth due to lack of food.

The observed changes in feeding behavior for the few days following the switch to a new shipment of J-5 drilling mud is another indication of the variability of the muds. Even when samples are collected simultaneously and stored under similar conditions, the animals clearly responded differently to the "new" mud.

The combined effects of chemical toxicity and the physical barrier of a covering layer of drilling mud are best seen in the tests on effects of substrate depth. A 4-mm layer of M-25 drilling mud covering the normal mud substrate caused serious problems for shelter construction in juvenile lobsters (which normally spend much of their first years inside substrate tunnels and crevices (J. Atema personal observation; R. A. Cooper personal communication). These problems resulted in reduced quality of burrows and increased time to find a burrow site. Some consequences at the population level may be increased exposure to predation, particularly by the large group of demersal fish predators, and displacement by bottom currents. Because similar effects on shelter construction were observed in the group of juveniles exposed to a 4-mm layer of the barite–bentonite mixture, it is likely that physical factors and not chemical toxicity caused this type of interference. However, in addition, chemical toxicity was probably responsible for the observed lethargy in DM-exposed animals; this would further increase their vulnerability to predation.

Together these experiments indicate that the effects of 4-mm covering layers of drilling mud are likely due to a combination of physical and chemical interference. This will now be evaluated further for 1-mm substrate cover.

Effects of water column toxicity are indicated in comparing Choice and No-Choice experiments. Both experiments resulted in significant delays in lobsters' starting to dig a shelter, but in No-Choice experiments the delay was significantly greater than in Choice, whereas the controls for both treatments did not differ significantly (Tables 3 and 4). In No-Choice treatment, the substrate is completely covered with a 1-mm layer using twice the amount of DM used to cover one-half the substrate in Choice treatment. Since before burrowing, the lobsters spent an equal amount of time on the clean and the layered side and built their burrows with equal frequency on either side in J-5, the greater delays in No-Choice may have been caused by the greater water column levels of toxic elements. The contribution of the physical effects of a 1-mm layer of DM may be further downplayed considering that in the corners of all tanks the covering layer of DM or BM was generally cleared away by the water inflows. The corners were almost always the places where the lobsters constructed a burrow. Moreover, in Disturbance tests, few animals evacuated their shelters when bay mud (BM) was dumped on their shelters, whereas far more evacuated with a dumping of DM (Table 5). Some physical effects, however, are indicated by the fact that the few animals that did leave their burrows after BM disturbance took as long as DM-disturbed animals to build a new shelter.

Chemical toxicity of drilling muds is further indicated in avoidance behavior, unprovoked tailflipping, lethargy, and shelter-digging delays. A remarkable similarity was observed in the types of toxic effects seen in some of the drilling mud exposures compared with petroleum hydrocarbon exposures (Atema and Stein 1974; Atema 1976; Atema et al. 1979; Wells and Sprague 1976). These effects include delays in feeding responses at 0.3 mg/L No. 2 fuel oil (water-accommodated fraction) and neurophysiological effects on chemoreceptors and neuromuscular problems at 1–2 mg/L exposures. It is important to know the petroleum content of the drilling muds.

These experiments were not designed to identify the toxic fractions or components of drilling muds. The muds used in these experiments were all collected after they had been used in the actual drilling operation, where high pressure and high temperatures can change their original composition considerably. At present, too little is known of the chemical composition of these "spent" muds. However, the range of toxic effects to one organism has now been described, and the methodology to test for toxicity in a variety of seminatural conditions has been defined. This should now make it possible to test systematically the toxicity and physical effects of any substrate-covering discharge.

The ecological consequences of the observed sublethal effects of drilling muds on juvenile lobsters can be predicted from these results in combination with knowledge of their natural behavior and local hydrography. Hydrographic and sedimentation studies of drilling mud discharge plumes are in their infancy. From the few data now available, we can surmise that water column levels of 10 mg/L exist inside plumes as far as 1 km from the source and that substrate cover of 1 mm can accumulate over areas of many square kilometres around the source (Adams 1978). Both water column dilution and substrate accumulation are greatly dependent on local conditions of water movement. "Sink" areas even far away from the source could easily accumulate heavy layers of discharged material. Even a 1-mm layer of DM covering the substrate causes delays in shelter construction and shelter quality. This effect increases with layer depth and a 4-mm layer makes shelter construction practically impossible. The animals are thus more exposed to predation. Lethargy makes them easier prey and unprovoked tailflipping makes them more obvious prey. Feeding delays put them at a competitive disadvantage, and molt delays and molt damage directly decrease the population. Thus, accumulation of drilling mud presents problems for benthic invertebrates, as demonstrated here for early juvenile lobsters during and after settling into a substrate.

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Environmental Regulation of Growth Rate, Efficiency, and Swimming Performance in Larval Capelin (*Mallotus villosus*), and its Application to the Match/Mismatch Hypothesis[1]

KENNETH T. FRANK AND WILLIAM C. LEGGETT

Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1

FRANK, K. T., AND W. C. LEGGETT. 1982. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the match/mismatch hypothesis. Can. J. Fish. Aquat. Sci. 39: 691 – 699.

We examined the influence of in situ environmental conditions on the growth rate, growth efficiency, and swimming ability of larval capelin (*Mallotus villosus*). Larval growth rate and efficiency prior to first feeding were strongly influenced by temperatures in the beach-rearing environment prior to dispersal. The interacting effects of water temperature and hours of sunlight (solar heating) on this intertidal habitat were the major regulators of growth ($R^2 \geq 0.96$). A model based on these parameters accurately predicted growth rates of larvae in the gravel sampled in two previous years. Larval condition at the time of dispersal into the pelagic environment was a negative function of the length of time spent in the beach gravel and of temperature conditions during that period. Swimming performance at dispersal was directly related to larval condition. Our data indicate that environmental conditions during the early (preexogenous feeding) period can influence growth efficiency, size attained at first feeding and the prey capture ability of larvae independent of the yolk reserves available at hatching, and the quantity and quality of the food available at the obligatory onset of exogenous feeding.

Key words: capelin, *Mallotus villosus*; growth rate, growth efficiency, swimming performance, larvae, intertidal zone, temperature

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Nous avons étudié l'influence des conditions du milieu in situ sur le taux et l'efficacité de croissance et la performance natatoire de larves de capelan (*Mallotus villosus*). Le taux et l'efficacité de la croissance larvaire avant le premier repas sont fortement influencés par les températures du milieu d'alevinage de la plage avant la dispersion. L'interaction de la température de l'eau et des heures d'ensoleillement (chaleur solaire) sur cet habitat intertidal est le principal facteur de contrôle de la croissance ($R^2 \geq 0{,}96$). Un modèle fondé sur ces paramètres a prédit avec précision les taux de croissance des larves dans un gravier échantillonné au cours de deux années précédentes. La condition des larves au moment de la dispersion dans l'environnement pélagique est fonction inverse de la durée du séjour dans le gravier de la plage et les conditions de températures durant cette période. La performance natatoire au moment de la dispersion est en relation directe avec la condition larvaire. Selon nos données, les conditions ambiantes du début (avant alimentation exogène) peuvent influer sur l'efficacité de croissance, la taille au moment de la première ingestion de nourriture et l'aptitude des larves indépendantes des réserves vitellines disponibles à l'éclosion à capturer des proies. Ces conditions influent également sur la quantité et la qualité de nourriture disponible au moment où l'alimentation exogène devient obligatoire.

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THE synchrony between hatching and first feeding of fish larvae and the occurrence of favorable food conditions has long been considered an important regulator of larval survival and year-class strength in fish. Direct evidence in support of this match/mismatch hypothesis (Cushing 1975) remains equivocal (May 1974); however, indirect support is given by the independent evolution of adaptations which ensure that spawning occurs and eggs hatch when feeding conditions are optimum (see Ware 1977).

A major difficulty confronting students of the match/mismatch hypothesis has been the extreme difficulty of quantifying the in situ developmental history of a single cohort from spawning to first feeding and beyond. Hence, relatively few studies have addressed the question of how in situ environmental conditions, operating through egg development rates and hatching times, influence synchrony. Equally poorly known is how in situ abiotic conditions experienced by larvae prior to complete yolk sac absorption influence the ability of larvae to exploit a given food resource assuming the required synchrony is achieved. In particular, it is possible that environmental conditions, through their influence on growth rate and efficiency, may regulate size at the obligatory onset of first feeding. This could modify the size spectrum of prey that can be used, the swimming and prey capture abilities of the larvae, etc., independent of the magnitude of the yolk reserves available at hatching (Ware 1975; Hunter 1972). Such differences would be the functional equivalent to the phenomenon of seasonal variations in egg diameter resulting in the production of larvae "of the right length, at the right time, which are well adapted to begin feeding on the existing size composition of the plankton" (Ware 1977).

The difficulties involved in quantifying the impact of environment on the in situ developmental history of a cohort has caused the major emphasis in studies to date to be directed toward quantifying the influence of variability in the timing of food availability, and its size structure and abundance, on the growth and survival of post yolk sac larvae (Jones 1973; Cushing 1974, 1975). We believe the influence of developmental history of larval fishes on their ability to exploit the food conditions experienced at first feeding may be an important component in the effective evaluation of the match/mismatch concept.

The unique early life history traits of capelin (*Mallotus villosus*) appear to provide an excellent system with which to examine this question. The capelin deposits its eggs on gravel beaches above the low tide line where they incubate and hatch (Templeman 1948). Egg development rate, hatching time, and mortality rates are predictable functions of incubation temperatures (Frank and Leggett 1981b). Hatching times vary between cohorts, being regulated by a complex of meteorological and hydrographic variables which control incubation temperatures (Frank and Leggett 1981b). Larvae accumulate in the gravel as they hatch and are released synchronously by onshore winds (Frank and Leggett 1981a) as concentrated "patches" (Frank and Leggett, unpublished data) which can be followed continuously for several days. Larval residence time in the gravel is variable and unpredictable, being determined by the interaction of egg development rates and the frequency of onshore winds. The physical condition of the larvae at release is a negative function of residence time (Frank and Leggett 1981a) and is believed to be further influenced by temperature conditions in the gravel during residence time. These parameters can be quantified precisely. This combination of characteristics makes possible a more rigorous in situ analysis of the effects of environmental conditions experienced by eggs and larvae prior to first feeding on time to first feeding, growth rates, growth efficiency, size at first feeding, and mortality rates. Our current research with capelin is directed towards a clearer understanding of how environment affects these parameters. In earlier studies we have documented the effect of abiotic variables on egg development rate and mortality (Frank and Leggett 1981b), the timing of the onset of larval drift (Frank and Leggett 1981a), and the food and predator field experienced by larvae at the onset of drift (Frank and Leggett 1982).

The purpose of this study was to identify the important predispersal environmental conditions regulating the growth rate and efficiency of capelin larvae, and to evaluate their effects. We chose to examine these parameters because they have obvious effects on size at first feeding and swimming ability which are known to influence predator avoidance, feeding ability and, in turn, survival (Blaxter and Hempel 1963; Lasker et al. 1970; Hunter 1972; Ware 1975).

Methods

STUDY AREA

The study was conducted at Bryant's Cove, Conception Bay, Newfoundland (47°40′36″N; 53°11′24″W). For a detailed description of the study site see Frank and Leggett (1981a). The spawning beach is typical in orientation and gravel size to most east coast spawning sites (Templeman 1948).

GROWTH RATES

The influence of predispersal rearing conditions on larval growth was assessed by in situ experiments and by sequential sampling of larvae from the beach gravel.

Three sets of in situ experiments were conducted in 1980. In each we stocked cylindrical plastic canisters (3 cm in diameter × 5 cm long), uniformly perforated with thousands of pinholes, with egg-bearing gravel and buried them at a depth of 4–6 cm in the beach gravel. The perforations allowed water and gas exchange but prevented exit or entry of eggs and larvae. Previous studies had shown (Frank and Leggett 1981b) that egg development rate and mortality does not vary with depth of deposition.

Eggs used in experiments 1 and 2 were collected immediately after the first and second spawnings and were all newly fertilized. In experiment 3 we used eggs collected at the low tide location of the beach where egg development rates are slowest (Frank and Leggett 1981b). An undetermined period of egg development had occurred prior to canister loading in this experiment. Experiment 1 (June 17–July 3) employed 46 canisters each stocked with 11–14 eggs/cm^3: 20 canisters buried at high tide (HT) and 26 at mid-tide (MT) locations. Experiment 2 (July 2–July 25) used 77 canisters each containing ~ 40 eggs/cm^3: 17 positioned at HT, 26 at MT, and 32 at low tide (LT) locations. Experiment 3 (July 24–August 4) employed 47 canisters each stocked with 11–14

eggs/cm^3: 20 placed at HT and 27 at MT. Our previous work (Frank and Leggett 1981b) showed that density effects on growth and mortality were insignificant at these densities (e.g. average densities in the beach gravel immediately after spawning range from 90 to 140 eggs/cm^3). The canisters were surrounded by a wooden enclosure, the top and bottom of which was sealed with wire mesh. This was done to prevent loss of canisters in the event of heavy wave action.

Canisters were checked daily beginning a few days before the predicted onset of hatching (Frank and Leggett 1981b). Beginning on the 1st day of hatching two canisters were removed daily from each beach location. Following swimming ability observations (see Swimming Ability) all larvae from each canister were preserved in 4% buffered Formalin. Median hatching times for each experiment were defined as the midpoint of the cumulative hatching frequency distribution (Alderdice and Forrester 1971).

The larvae varied in physical condition at the time of sampling (see also Frank and Leggett 1981a). We defined five categories of condition: (1) robust larvae obviously in good condition, straight transparent body; (2) body losing transparency, developing a whitish appearance; (3) slight spinal curvature evident, body depth and transparency lessening; (4) extreme spinal curvature, usually just posterior to the head or anterior to tail region, body more white than transparent, body depth reduced; (5) body coloration white, obvious loss of muscle integrity, thinning.

Total length and yolk sac size measurements were made on 20 or more category 1 larvae from each canister. Yolk sac size was graded on a five-point scale where 4 represented a full yolk and 0 no yolk sac remaining. This and all other subjective evaluations were made by a single observer to reduce variability in the data. Growth rates of larvae in the canisters were determined by least squares regressions of total length of all larvae sampled on a given day against time. Day 1 was set at the start of hatching.

We also assessed growth rates of larvae in the beach gravel. We collected larvae twice weekly at each of the HT, MT, and LT locations in both 1978 and 1979. Triplicate samples were taken at each location in 1978 and duplicate samples were taken in 1979. Two separate spawnings occurred in both years. Growth estimates were thus obtained for four separate larval cohorts. All sampling was conducted during daylight hours and at the time of low tide. Samples were taken with a 5.5-cm ID steel corer. Full details of the sampling method are provided in Frank and Leggett (1981a). Cores ranged in depth from 10 to 16 cm and were preserved in 4% buffered Formalin as discrete 2-cm slices. Total length was determined for at least 50 larvae from each 2-cm slice. Only category 1 larvae were measured.

Analysis of growth rates of larvae in the sediments by sequential sampling is complicated by the fact that larvae accumulate in the gravel during offshore wind conditions and are then released, at irregular and unpredictable intervals, by onshore wind-generated wave action (Frank and Leggett 1981a). Hence, the mean age (days posthatching) and size of larvae in the gravel varies considerably over time being greatest just before and least immediately after releases. To eliminate this bias we included in our analysis only those time intervals during which significant ($P < 0.05$) positive increases in length occurred. In only 2 of 11 such intervals was the beach subjected to onshore winds capable of causing release of larvae.

Growth in millimetres per day was determined for each time interval. These values were compared with growth rates predicted from equations, developed from the container experiments, relating larval growth rates to the important environmental regulators. In this analysis we lagged the growth rates 1 d behind the temperature/sunlight data. This 1-d lag was employed to ensure that environmental conditions influencing growth over the full 24 h preceding initial and final sampling days were incorporated in the prediction.

Growth Efficiency

We examined the hypothesis that differences in growth rates between larvae in the three canister experiments and in situ (see below) reflected differences in growth efficiency (mm growth/unit energy) resulting from the different beach gravel conditions experienced. We compared the rate of change in length in the various experiments (growth) with the degree of yolk sac absorption. The assumption implicit in this analysis is that yolk volume is a reliable estimator of the energy reserve available to the larvae. The method of quantifying yolk sac volume produced a discontinuous variable which was subjected to least squares regression, a procedure which in certain circumstances is statistically questionable. In this instance we believe the approach was justifiable because the resulting relationships were used solely to obtain an objective estimate of (1) the degree of change (growth) associated with the level of yolk energy available to larvae and (2) the rate of yolk use in each experiment.

Swimming Ability

The physical condition of larval capelin is an inverse function of predispersal residence time in the beach sediments (Frank and Leggett 1981a). The proportion of category 1 larvae released from the gravel in 1978 and 1979 varied from 91% at 1 d postmedian hatching to 22% at 8.5 d postmedian hatching. Therefore, we evaluated the relationship between swimming ability and larval condition. When individual canisters used in the growth experiments were sampled, their contents were immediately emptied into a circular observation tank (18 cm in diameter × 10 cm deep) which was half filled with recently collected seawater. This procedure mimics the transition from gravel residence to pelagic existence experienced by larvae during onshore winds both in its abruptness and in changes in thermal conditions that might be experienced. The behavior of up to 10 individual larvae from each canister was recorded for 1−2 min. We recorded three categories of behavior: coordinated swimming, aberrant movement, and resting. Coordinated swimming was characterized by integrated tail and head movements which enabled the larvae to maintain their position in the water column. Aberrant movement was characterized by irregularity in head and tail beat frequency and resulted in sporadic motion rather than directed swimming. Some larvae in this category appeared to be moving all parts of the body simultaneously which gave the impression of totally uncoordinated movement. Resting was defined as the interval between swimming bouts when larvae were gliding or were lying upright on the bottom. All obser-

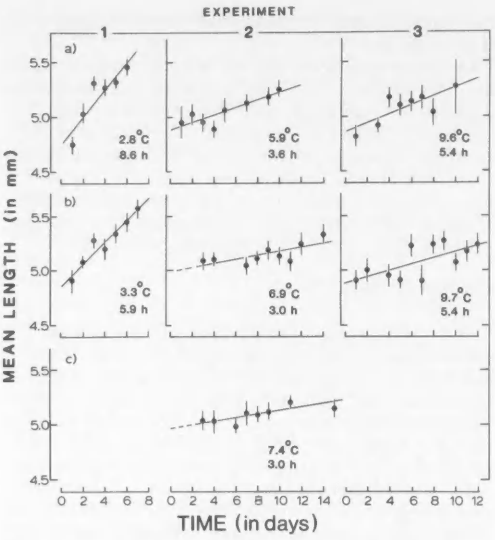

FIG. 1. Relationship between larval size (Y, mm) and posthatching residence time (X, d) derived from in situ experiments at: a) HT (high tide): Exp. 1, $Y = 4.75 + 0.125\,X$, $R^2 = 0.83$; Exp. 2, $Y = 4.88 + 0.034\,X$, $R^2 = 0.77$; Exp. 3, $Y = 4.86 + 0.040\,X$, $R^2 = 0.61$. b) MT (mid-tide): Exp. 1, $Y = 4.86 + 0.100\,X$, $R^2 = 0.93$; Exp. 2, $Y = 4.99 + 0.018\,X$, $R^2 = 0.50$; Exp. 3, $Y = 4.88 + 0.029\,X$, $R^2 = 0.48$. c) LT (low tide): Exp. 2, $Y = 4.97 + 0.016\,X$, $R^2 = 0.64$. All regressions are statistically significant ($P < 0.05$). The mean daily hours of sun and water temperature conditions during each experiment are shown. Vertical bars indicate 95% C.I.

vations relating to the type and duration of each activity were recorded on magnetic tape, and the physical condition of the larvae under observation (based on the five-point scale previously defined) was noted.

Results

GROWTH RATE

Analysis of covariance revealed significant heterogeneity ($P < 0.001$) between the slopes of the length/time regressions calculated for the three canister experiments (Fig. 1).

We hypothesized that these growth differences were mediated by temperature conditions during residence in the beach gravel. Water temperature, hours of sunlight, and maximum and minimum air temperature are the major regulators of temperature conditions in the gravel. Air temperatures and hours of sunlight are the major regulators of temperatures in the beach gravel at high tide when the beach is exposed. Water temperature is the major regulator at low tide. Hours of sunlight has a significant influence because of solar heating (Frank and Leggett 1981b). Water temperatures and hours of sunlight also appear to be interrelated. The temperature of the inshore water mass is significantly influenced by wind conditions; onshore winds cause warm surface waters to dominate, offshore winds cause deep colder waters to upwell in the

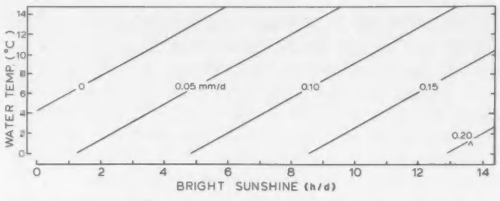

FIG. 2. Contour plot of larval growth rate predicted from Eq. 1. This figure shows that growth rates increased with decreasing water temperature and increasing hours of bright sunshine.

inshore area (Frank and Leggett 1982). Offshore winds are more frequently associated with high atmospheric pressure zones, hence hours of sunshine and water temperatures are negatively associated. We have previously shown that these variables are major regulators of metabolic processes in the egg stage, explaining >85% of the variance in egg development rates at all levels on the beach (Frank and Leggett 1981b).

We conducted a stepwise multiple regression analysis of daily growth rates (the slope of the length/time regressions) against the mean daily water temperature, mean daily hours of sunlight, and mean daily maximum and minimum air temperatures during the interval from onset of hatching to the termination of the experiment. Only water temperatures (X_1) and hours of sunlight (X_2) entered the regression. These two variables accounted for 98% ($n = 7$, $P < 0.001$) of the between experiment, between location variance in growth rates. The equation to predict growth rate (Y, mm/d) is:

$$(1)\quad Y = 0.033 - 0.008\,X_1 + 0.014\,X_2.$$

Alone, water temperature and hours of sunlight explained 65 and 78% of the variance in growth rate, respectively. Growth rates were greatest during combinations of low water temperatures and maximum hours of sunlight (Fig. 2). We conclude that predispersal growth rate is a function of temperature conditions in the gravel being regulated principally by water temperature and solar heating.

Nine of 11 growth rates determined for larvae at liberty in the gravel were strongly correlated with the rates predicted from the canister experiments (intercept = −0.001, slope = 0.99; $r = 0.86$, $P < 0.01$). Two predicted rates exceeded the observed by an order of magnitude during a 4-d period in late July, 1978, which was characterized by low water temperatures and a maximum number of hours of sunlight (>10).

GROWTH EFFICIENCY

Growth efficiency, like growth rate, varied between container experiments and was linked to conditions in the gravel (Fig. 3). Mean water temperature (X_1) and mean hours of sunlight (X_2) during the interval from first hatching to termination of the experiments explained 96% ($n = 7$, $P < 0.001$) of the variance in growth efficiency between experiments. The equation to predict growth efficiency (Y, mm/unit of yolk) is:

$$(2)\quad Y = 0.140 - 0.009\,X_1 + 0.005\,X_2.$$

Water temperature and hours of sunlight explained 87 and

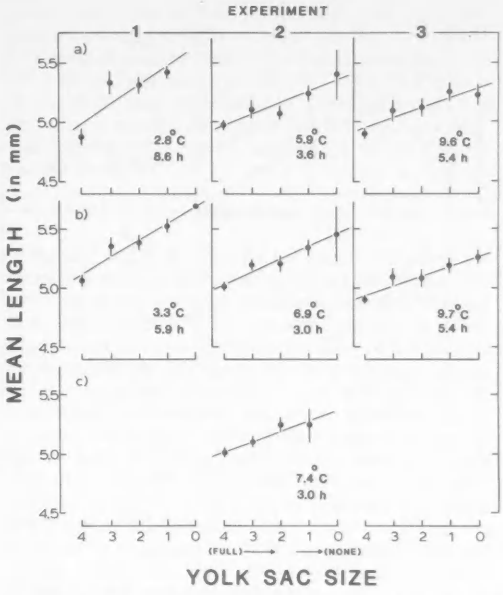

FIG. 3. Larval length (Y, mm) attained at each of five grades of yolk sac size (X) from in situ experiments at: a) HT: Exp. 1, $Y = 4.99 + 0.159\,X$, $R^2 = 0.72$; Exp. 2, $Y = 4.97 + 0.097\,X$, $R^2 = 0.90$; Exp. 3, $Y = 4.95 + 0.082\,X$, $R^2 = 0.86$. b) MT: Exp. 1, $Y = 5.11 + 0.146\,X$, $R^2 = 0.94$; Exp. 2, $Y = 5.03 + 0.105\,X$, $R^2 = 0.96$; Exp. 3, $Y = 4.94 + 0.082\,X$, $R^2 = 0.90$. c) LT: Exp. 2, $Y = 5.02 + 0.083\,X$, $R^2 = 0.90$. All regressions are statistically significant ($P < 0.05$). To solve for Y, convert values of X to $|X - 4|$. The mean daily hours of sun and water temperature conditions during each experiment are shown. Vertical bars indicate 95% C.I.

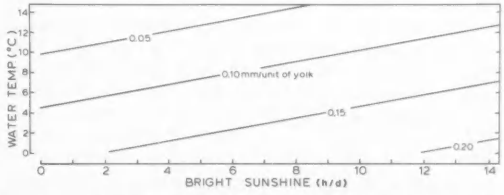

FIG. 4. Contour plot of growth efficiency predicted from Eq. 2. This figure shows that growth efficiency increased with decreasing water temperature and increasing hours of bright sunshine.

49% of the variance in growth efficiency, respectively, when each variable was entered alone into the regression. Growth efficiency, like growth rate, was greatest during conditions characterized by low mean water temperature and maximum hours of sun (Fig. 4).

SWIMMING ABILITY

The time spent in coordinated swimming declined as larval condition deteriorated; the time spent in uncoordinated swimming increased as condition deteriorated; and time spent resting did not vary greatly with larval condition (Fig. 5). A modest drop in larval condition (from category 1 to 2) produced the greatest change in behavior with time spent in active swimming declining from 73 to 34% and time spent resting increasing from 26 to 43%. Subsequent changes in behavior relative to condition were less pronounced.

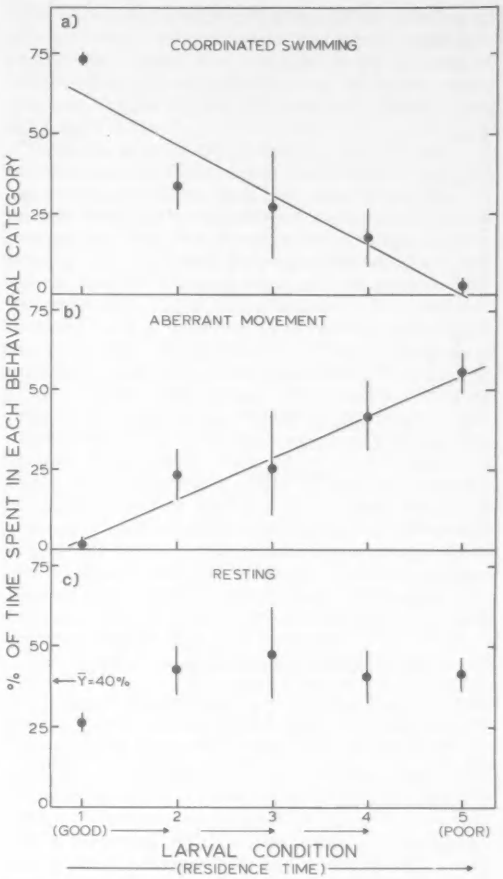

FIG. 5. The effect of physical condition (X; a negative function of posthatching residence time) on the percentage of time larvae spent in each of three behavioral categories (Y). Equations for the regression lines are a) $Y = 78.1 - 15.72\,X$, $R^2 = 0.89$, $P < 0.01$. b) $Y = -9.3 + 12.85\,X$, $R^2 = 0.95$, $P < 0.01$. c) $R^2 = 0.32$, ns. Vertical bars show 95% C.I.

Because the thermal experience of the larvae prior to release from the gravel may influence swimming ability independent of larval condition, we also evaluated the effect of temperature on swimming ability. We regressed the percentage of time spent in active swimming (arcsine transformed to normalize the data) against beach gravel temperatures immediately prior to removal from the gravel (Fig. 6). For this analysis we used only category 1 larvae. Larvae from all three beach locations (HT, MT, LT) exhibited reduced swimming

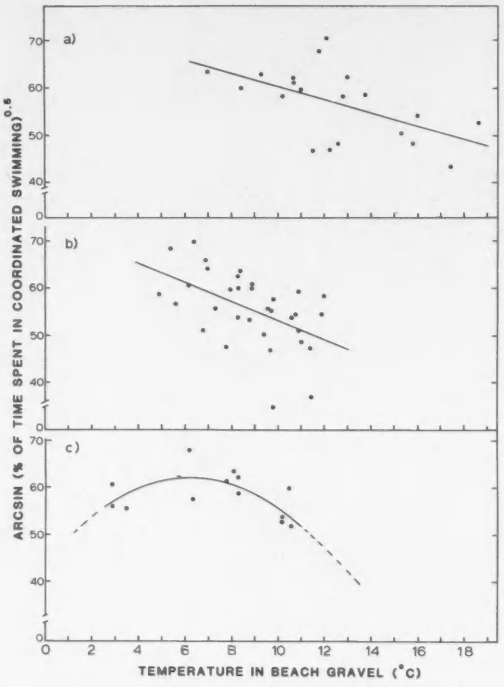

FIG. 6. The effect of beach gravel temperature (X, average of daily temperature conditions on day prior to and on the day of observation) on swimming activity (Y) of category 1 larvae originating from a) HT, $(\sin Y)^2 = 74.4 - 1.42\,X$, $R^2 = 0.31$, $P < 0.05$; b) MT, $(\sin Y)^2 = 73.6 - 2.03\,X$, $R^2 = 0.26$, $P < 0.01$; c) LT, $(\sin Y^2) = 44.2 + 5.83\,X - 0.46\,X^2$, $R^2 = 0.46$, $P < 0.05$.

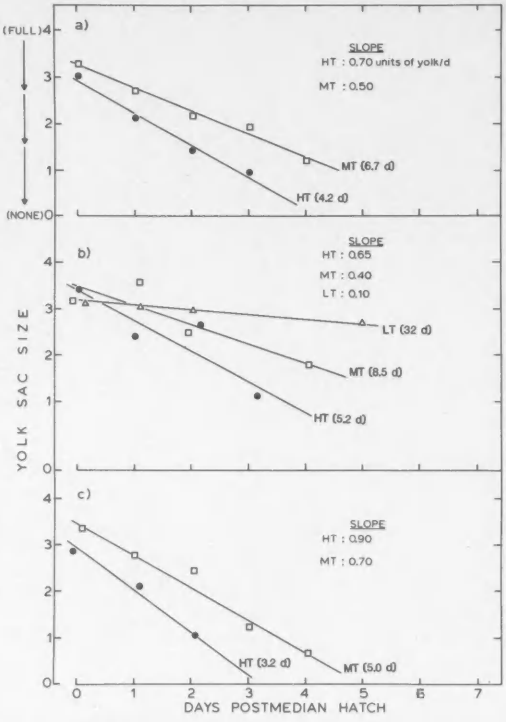

FIG. 7. Relationships between yolk sac size and time. Least squares derived slopes show changes in the rate of decline in yolk size between experiments a) 1, b) 2, and c) 3 and intertidal locations HT (●), MT (□), and LT (△). Extrapolated values in parentheses indicate the time in days to complete (zero) yolk absorption.

activity as temperatures increased. The proportion of time spent in coordinated swimming by category 1 larvae seldom declined below 50% as a result of temperature change. The effect of temperature on coordinated swimming ability was thus slight, relative to the effect of larval condition (Fig. 5).

Residence Time vs. Yolk Use and Larval Condition

Capelin beaches are inundated for brief periods during each day. For this reason we hypothesized that the majority, if not all, of the metabolic requirements of the larvae are met by energy stored in the yolk sac. We evaluated this idea by regressing yolk sac size vs. days postmedian hatch. Significant negative relationships were consistently observed (Fig. 7). Slopes varied between sites and experiments, possibly due to temporal and spatial differences in the predispersal habitat. Rates of yolk sac absorption were consistently highest at HT, intermediate at MT, and lowest at LT. A multiple regression of the slope of the yolk sac size/time relationships against mean water temperature (X_1) and mean hours of sunlight (X_2) was not statistically significant ($n = 7$, $P < 0.2$). However, a plot of the interaction of these variables (Fig. 8) is in general agreement with earlier findings regarding growth efficiency, and with the general metabolic response of

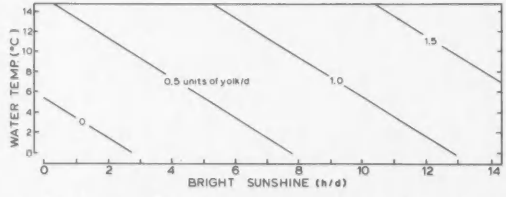

FIG. 8. Contour plot of the rate of change in yolk size predicted from Eq. 3. This figure shows that rates of yolk use increased with increasing water temperature and increasing hours of bright sunshine.

poikilotherms to temperatures (i.e. rate of yolk sac use was positively related to water temperature and hours of sunlight). The equation to predict the rate of change in yolk size (Y, units of yolk/d) is:

$$(3) \quad Y = -0.288 + 0.0516\,X_1 + 0.1036\,X_2.$$

It is also possible that the differences in rates of yolk absorption while the larvae are resident in the beach is influenced in part by differences in the availability of exogenous food. The low tide zone, where rates are lowest, is inundated for the

greatest interval in any 24-h period. During inundation suspended food is theoretically available. This may contribute to the inverse relationship between duration of inundation LT > MT > HT and yolk absorption rates HT > MT > LT. Extrapolation of the linear relationships between yolk sac size and time (Fig. 7) suggests the time to complete yolk sac absorption varies between 3.2 and 8.5 d (mean 5.5, SE 0.8) at the HT and MT locations.

Discussion

We have shown that growth rate, growth efficiency, and swimming ability of larval capelin are influenced in predictable ways by environmental conditions during their residence in the beach gravel. The principal regulators of these biological parameters are water temperature, hours of sunlight, and the duration of the interval between onshore winds. Because the eggs are located above the LT zone on the beach, both water temperature and hours of sunlight (solar heating) are important determinants of beach temperatures and hence of the rate and efficiency of metabolic processes of the eggs (Frank and Leggett 1981b) and early larval stages (this study) of capelin in the beach gravel. The duration of the interval between onshore winds determines the length of time during which larvae are influenced by these conditions (Frank and Leggett 1981a) and, hence, their condition at the time of release into the pelagic environment.

Growth Rate and Efficiency

Growth rate and efficiency of capelin larvae during their residence in the beach gravel are readily and accurately predictable from measures of water temperature and hours of sunshine. Growth rate and efficiency were not, however, significantly related to average beach gravel temperatures ($r = -0.04$), but were more directly linked to water temperatures and hours of sunlight. This suggests that both growth rate and efficiency may be influenced more directly by shorter term temperature conditions in the gravel. A similar short-term response to environmental conditions is evident in egg mortality rates in capelin. Egg development rates, in contrast, are primarily regulated by average temperature conditions in the gravel prevailing during the incubation period (Frank and Leggett 1981b).

The negative relationship between growth rate and efficiency and temperature demonstrated for larval capelin is consistent with the results of several earlier studies involving a variety of fish species. Yolk utilization efficiency was found to be maximal near the lower limit of the normal range of development temperatures in *Salmo fario*, 3–12°C (Gray 1929); sole, *Solea solea*, 10–20°C (Flüchter and Pandian 1968); Pacific herring, *Clupea harengus pallasii*, 4–10°C (Alderdice and Velsen 1971); Pacific cod, *Gadus macrocephalus*, 3–10°C (Alderdice and Forrester 1971); tautog, *Tautoga onitis*, 16–22°C (Laurence 1973); Atlantic salmon, *Salmo salar*, 2–12°C (Peterson et al. 1977).

Growth rate and efficiency have a direct influence on size at release and at complete yolk sac absorption because for any given larval residence time, size will be greatest when rate and efficiency are maximum. In general, this is achieved when water temperatures are lowest, a condition which occurs during offshore wind conditions that induce the upwelling of deep cold water. Offshore winds (west through southwest) dominate the summer wind conditions on the east coast of Newfoundland and the Labrador coast, the major inshore spawning areas for capelin in the northwest Atlantic (Frank and Leggett 1981a).

Variations in size at release resulting from differences in environmental conditions during beach residence, and the variable residence times, may have major implications for survival. Ware (1975) demonstrated a positive relationship between growth rate and survival in larvae of plaice (*Pleuronectes platessa*), haddock (*Melanogrammus aeglefinus*), and Atlantic mackerel (*Scomber scombrus*). He concluded that this relationship resulted from a reduction in the number of predatory fields to which the larvae were exposed and an increase in the size spectrum of the prey they were capable of exploiting as they grew. Similar relationships have been reported by Marak (1960), Sysoeva and Degtereva (1965), and Sherman and Honey (1971). In addition, searching and prey capture ability is known to increase rapidly with initial growth (Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972). For example, solving Hunter's (1972) equation for searching volume yielded a 20% difference in volume searched given the 0.5-mm variation in size of capelin larvae at zero yolk (= time of first feeding) between experiments (Fig. 3). Similarly, Ryland (1963) found that a 10% variation (induced by temperature) in larval size of a 7.0-mm plaice, *P. platessa*, corresponded to a 10–25% increase in swimming and burst speeds.

The survival of capelin larvae may also be dependent on the rate of yolk sac use (a function of growth efficiency) and the duration of the beach residence period which is governed by the frequency of onshore winds. When growth efficiency is low, and/or onshore winds infrequent, complete yolk sac absorption can occur prior to release resulting in death in the gravel or the release of severely weakened larvae. The average interval between onshore winds (N through E) in June and July as calculated from 15 yr of data (1966–80) from the St. John's (Nfld.) weather station was 4.2 d (SD = 2.63, $n = 64$; range: 1–13 d). This compares with an estimated average time to complete yolk sac absorption of 3.5 d at HT sites and 6.7 d at MT sites. Variance in the interval between onshore winds can account for a 20% difference in mean length at release. The survival implications of this difference have been discussed above. In addition, residence times in excess of 4.2 and 6.7 d can be expected to have significant impacts on the physical condition of larvae released from the HT and MT zones, respectively, because these larvae would be forced to consume body tissues to support their metabolic needs. We have previously reported (Frank and Leggett 1981a) a negative correlation between the condition of larvae in the beach gravel and the intertidal water mass and the length of the interval between onshore winds.

Swimming Ability

The proportion of larvae in poor condition declines sharply over the first 15–20 m from the beach (intertidal to nearshore; Frank and Leggett 1981a). We hypothesized that this reduction occurs because these weakened larvae suffer an increased susceptibility to predation. The strong negative correlation

between larval activity and condition is consistent with this hypothesis. Swimming ability was strongly depressed by deteriorating physical condition. Bams (1967), Lillelund and Lasker (1971), Theilacker and Lasker (1974), and Hunter (1972) have all demonstrated a strong negative relationship between death due to predation and swimming performance. In addition, feeding efficiency is positively correlated with swimming ability (Laurence 1972; Rosenthal and Hempel 1970). Hence, weakened larvae would grow less rapidly and remain vulnerable to predators for a greater period of time thereby increasing their mortality rates (Ware 1975). Also, declining physical condition in capelin larvae and the corresponding increase in sporadic and irregular swimming motion may increase their susceptibility to predators that use vibrational cues to detect their prey, a notable example being chaetognaths (Newbury 1972).

The influence of beach gravel temperatures on swimming ability following release was less pronounced than that of larval condition, but was, nevertheless, significant. Activity levels following release were consistently depressed as temperatures increased above ~8°C.

In summary, our data indicate that environmental conditions during early (preexogenous feeding) larval development can influence growth rate and efficiency, size at first feeding, and the prey capture ability of larvae independent of the magnitude of the yolk reserve available at hatching, and the quantity and quality of the food available at the obligatory onset of exogenous feeding. This finding supports our view that a greater knowledge of the effect of environment on the developmental history of fishes prior to first feeding is an important component in the effective evaluation of the match/mismatch hypothesis. We further suggest that future tests of the match/mismatch hypothesis should incorporate an evaluation of those environmental variables (e.g. water temperature) known to regulate both the productivity and size composition of the plankton (Ware 1977) and the developmental parameters of the eggs and larvae prior to the onset of first feeding.

Acknowledgments

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PCB Uptake by Five Species of Fish in Lake Michigan, Green Bay of Lake Michigan, and Cayuga Lake, New York[1]

A. L. JENSEN[2]

School of Natural Resources, University of Michigan, Ann Arbor, MI 48109, USA

AND S. A. SPIGARELLI AND M. M. THOMMES

Ecological Sciences Section, Radiological and Environmental Research Division, Argonne National Laboratory, Argonne, IL 60439, USA

JENSEN, A. L., S. A. SPIGARELLI, AND M. M. THOMMES. 1982. PCB uptake by five species of fish in Lake Michigan, Green Bay of Lake Michigan, and Cayuga Lake, New York. Can. J. Fish. Aquat. Sci. 39: 700–709.

We applied a bioenergetic model to describe uptake of polychlorinated biphenyls (PCBs) by lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), lake whitefish (*Coregonus clupeaformis*), coho salmon (*Oncorhynchus kisutch*), and chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan; lake trout and lake whitefish in Green Bay of Lake Michigan; and lake trout in Cayuga Lake, New York. The model describes PCB uptake in terms of metabolism, food consumption, size, and growth. Concentrations of PCBs differ significantly among species; for the same species there are large differences among habitats. The pattern of PCB uptake by brown trout is different from that of the other species. Application of the model with uptake and metabolic parameters estimated by Norstrom et al. describes the trend in the brown trout data; to describe uptake for other species we increased the exponent of weight for metabolism γ. An increase in γ changes the shape of the relation between PCB concentration and body weight from asymptotic to non-asymptotic. In all species tested except brown trout, uptake of PCBs was not asymptotic and concentrations did not approach an equilibrium; accumulation of contaminants was first rapid, decreased toward a plateau, and then began a second rapid increase. Simulation studies indicate that differences in PCB concentrations among species and in the same species among different environments result from differences in metabolic parameters, exposure, size, and rate of growth.

Key words: PCBs, bioenergetic model, contaminant uptake, toxicology, fish, Great Lakes, salmon, trout, whitefish

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Un modèle bioénergétique a servi a décrire l'absorption des biphényls polychlorés (BPC) chez les espèces suivantes : touladi (*Salvelinus namaycush*), truite brune (*Salmo trutta*), grand corégone (*Coregonus clupeaformis*), saumon coho (*Oncorhynchus kisutch*) et saumon chinook (*Oncorhynchus tshawytscha*) dans le lac Michigan; touladi et grand corégone dans la baie Verte du lac Michigan; et touladi dans le lac Cayuga (New York). Le modèle décrit l'absorption des BPC en termes de métabolisme, de consommation de nourriture, de taille et de croissance. Les concentrations de BPC diffèrent nettement d'une espèce à l'autre; et dans une même espèce, il y a de grandes différences entre habitats. Les caractéristiques de l'absorption des BPC par la truite brune diffèrent de celles des autres espèces. Si l'on applique le modèle aux paramètres d'absorption et de métabolisme estimés par Norstrom *et al.*, il apparaît une tendance dans les données sur la truite brune; pour décrire l'absorption chez les autres espèces, nous augmentons l'exposant du poids pour métabolisme γ. Une augmentation de γ modifie la forme de la relation entre la concentration des BPC et le poids corporel : d'asymptotique qu'elle était, elle devient non asymptotique. Chez toutes les espèces testées, sauf la truite brune, l'absorption des BPC n'est pas asymptotique, et les concentrations n'atteignent pas un état d'équilibre; l'accumulation des contaminants est rapide au début,

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diminue vers un plateau, pour ensuite commencer une nouvelle augmentation rapide. Des études de simulation indiquent que des différences de paramètres métaboliques, d'exposition, de taille et de taux de croissance sont responsables de différences de concentration de BPC entre espèces et chez une même espèce habitant différents environnements.

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LARGE differences in polychlorinated biphenyl (PCB) concentrations are commonly observed among different species in the same environment and in the same species among different environments. For example, concentrations of PCBs in lake trout (*Salvelinus namaycush*) are much higher than those in brown trout (*Salmo trutta*) and other species of Lake Michigan fishes (Scheffy 1977). Concentrations of PCBs in lake whitefish (*Coregonus clupeaformis*) are higher in Green Bay than in Lake Michigan, but concentrations in lake trout are a little higher in Lake Michigan than in Green Bay. In Lake Michigan PCB concentrations in coho salmon (*Oncorhynchus kisutch*) are lower than concentrations in chinook salmon (*Oncorhynchus tshawytscha*) even though both inhabit the same areas and consume the same foods. In Lake Michigan concentrations of PCBs in salmon are much lower than concentrations in lake trout.

These differences are explored by simulation of PCB uptake by these species under conditions found in Green Bay, Lake Michigan, and Cayuga Lake. The model applied is a bioenergetic model that describes uptake in terms of food consumption and respiration; these factors are related metabolically to size and growth rate. The model can be applied to different species and environments with little modification.

The Model

The Norstrom et al. (1976) model is based on the mass balance equation

$$(1)\quad \frac{dP}{dt} = e_{\mathrm{pf}} C_f R + e_{\mathrm{pw}} C_w V - kPW^{\xi}$$

where: P = body burden of pollutant in fish (g)
W = wet weight of fish (g)
e_{pf} = efficiency of assimilation of pollutant from food
e_{pw} = efficiency of assimilation of pollutant from water
C_f = concentration of pollutant in food (g/g)
C_w = concentration of pollutant in water (g/g)
R = ration, rate of food consumption (g/wk)
V = rate of water flow past the gills (g/wk)
k = clearance coefficient ($g^{-\xi}$/wk)
ξ = exponent of body weight in the clearance term.

Equation (1) states that change in body burden of a toxicant equals the rate of uptake from food, $e_{\mathrm{pf}} C_f R$, plus the rate of uptake from water, $e_{\mathrm{pw}} C_w V$, minus the rate of loss kPW^{ξ}.

An expression for ration was developed from the energy balance equation

$$(2)\quad e_f q_f R = Q + q_a \, dW/dt$$

where: e_f = efficiency of assimilation of metabolizable energy from food
q_f = joule equivalent of food (J/g)
q_a = joule equivalent of animal accumulating pollutant (J/g)
Q = total metabolic rate (J/wk).

Norstrom et al. (1976) separated total metabolic rate into a low-routine metabolic rate Q_{lr}, which includes the standard metabolic rate and the energy cost of spontaneous activity, and into the energy cost specific to utilization of food, Q_s. Application of the conventional metabolic expressions $Q_{\mathrm{lr}} = \alpha W^{\gamma}$ and $Q_s = \beta q_a \, dW/dt$ for these components gives

$$(3)\quad R = \frac{1}{e_f q_f} [\alpha W^{\gamma} + q_a(1 + \beta) \, dW/dt].$$

An expression for the volume of water passing the gills is found from the relation between the amount of oxygen necessary to satisfy metabolic demand and the volume of water containing this quantity of oxygen, which is

$$(4)\quad Q = e_{\mathrm{ox}} C_{\mathrm{ox}} q_{\mathrm{ox}} V$$

where: e_{ox} = efficiency of assimilation of oxygen by the gills
C_{ox} = concentration of oxygen in the water (g/g)
q_{ox} = joule equivalent of oxygen (J/g).

Application of the expression for Q given above (equation 4) gives

$$(5)\quad V = \frac{\alpha W^{\gamma} + \beta q_a \, dW/dt}{e_{\mathrm{ox}} C_{\mathrm{ox}} q_{\mathrm{ox}}}.$$

Substitution of the expressions for V and R into the mass balance equation gives

$$(6)\quad \frac{dP}{dt} = \frac{e_{\mathrm{pf}} C_{\mathrm{pf}}}{q_f e_f} [\alpha W^{\gamma} + q_a(1 + \beta) \, dW/dt] + \frac{e_{\mathrm{pw}} C_w}{e_{\mathrm{ox}} C_{\mathrm{ox}} q_{\mathrm{ox}}} [\alpha W^{\gamma} + \beta q_a \, dW/dt] - kPW^{\xi}.$$

To apply the uptake model, expressions for weight W and growth rate dW/dt are necessary. Growth was modeled using von Bertalanffy's equation

$$(7)\quad \frac{dW}{dt} = bKW_{\infty} e^{-Kt} (1 - e^{-Kt})^{b-1}$$

$$W(t) = W_{\infty} (1 - e^{-Kt})^{b}$$

TABLE 1. Description of uptake parameters and estimates. All estimates are from Norstrom et al. (1976).

Symbol	Description	Units	Value
e_{ef}	Efficiency of assimilation of metabolizable energy from food	—	0.82
e_f	Efficiency of assimilation of toxicant from food	—	0.80
e_w	Efficiency of assimilation of toxicant from water	—	0.75
β	Coefficient relating growth rate to energy associated with growth	—	1.0
γ	Exponent of body weight for metabolism	—	0.80
C_{ox}	Concentration of oxygen in the water	g/g	9.20×10^{-6}
q_{ox}	Joule equivalent of oxygen	$J \cdot g^{-1}$	1.43×10^4
k	Clearance coefficient	$g^{-\xi} \cdot wk^{-1}$	0.238
ξ	Exponent of body weight in clearance equation	—	0.58
α	Low-routine metabolism	$J \cdot wk^{-1} \cdot g^{-1}$	502.8
q_a	Joule equivalent of animal under study	$J \cdot g^{-1}$	4.19×10^3
q_f	Joule equivalent of food	$J \cdot g^{-1}$	4.19×10^3

where: W_∞ is the asymptotic weight, K is a growth coefficient, and b is a parameter of the length–weight equation. The growth equation was applied together with equation (6) to predict uptake of PCBs. For calculation of PCB concentrations as a function of time, equation (6) was replaced with a difference equation and a time interval of 1 h was used for calculations.

Data Description

Measurements of PCBs and total lengths of fish collected from Wisconsin waters of Lake Michigan and Green Bay were reported by the Wisconsin Department of Natural Resources (Sheffy 1977). Fish collected in harbor areas were not included in these analyses because tributaries are a major source of PCB contamination, and the level of contamination was higher in the few fish obtained from these areas. Observations were for the years 1974–77 when PCB concentrations were relatively constant; a regression of PCBs against time was not significant for either Lake Michigan or Green Bay.

Twenty PCB and length measurements were made on lake whitefish in Lake Michigan and 27 were made in Green Bay. One measurement in Green Bay was an outlier and was not included in the analyses. Eighty-nine PCB and length measurements were available for lake trout in Wisconsin waters of Lake Michigan and 42 measurements were available for Green Bay. Twenty-nine measurements were made on brown trout from Lake Michigan. Twenty-two PCB and length measurements were available for coho salmon in Lake Michigan. One observation was far different from the others, and it was not included in the analyses. Seventeen PCB and length measurements were available for chinook salmon in Lake Michigan.

All measurements in Green Bay and Lake Michigan were made on edible portions. The model is based on body burdens. Ten analyses on both body burden and edible portions were made for lake trout in Lake Michigan (Scheffy 1977), and the concentrations were not statistically different so no adjustment was made.

Twenty-four measurements of whole body PCB concentrations and body weight for lake trout of Cayuga Lake were reported by Bache et al. (1972).

Parameter Estimation

Growth parameters for lake trout and lake whitefish in Cayuga Lake, Green Bay, and Lake Michigan were initially estimated with data summarized by Carlander (1969). The data for Lake Michigan reported by Carlander (1969) were made before the increase in alewife (*Alosa pseudoharengus*) abundance that occurred in the late 1960's, and the growth rates were too low. The growth parameters were adjusted slightly to predict weights that have been observed more recently in Lake Michigan (Bails and Patriarche 1974). The length–weight relations applied to calculate weights for lake whitefish were $\log_{10} W = -5.98 + 3.36 \log_{10} L$ for Lake Michigan and $\log_{10} W = -6.03 + 3.38 \log_{10} L$ for Green Bay. For lake whitefish the parameter estimates for the growth equations were $W_\infty = 6$ kg and $K = 0.30$ yr^{-1}. The length–weight relation applied for lake trout in Lake Michigan and Green Bay was $\log_{10} W = -5.39 + 3.12 \log_{10} L$. For Cayuga Lake, weights were reported by Bache et al. (1972), and a conversion of length to weight was unnecessary.

The estimates of the growth parameters for lake trout in Green Bay and Lake Michigan were $W_\infty = 7.34$ kg and $K = 0.14$ yr^{-1} and in Cayuga Lake they were $W_\infty = 5.94$ kg and $K = 0.16$ yr^{-1}.

The growth parameters for salmon were estimated from age, length, and weight data for salmon collected at Straw-

berry Creek in Wisconsin (Daly et al. 1975). For coho salmon the length–weight relation for 630 fish was $\log_{10} W = -4.57 + 2.84 \log_{10} L$. The estimates of the parameters of the growth equation were $W_\infty = 5.27$ kg and $K = 0.58$ yr^{-1}. For chinook salmon the length–weight relation for 412 fish was $\log_{10} W = -4.86 + 2.97 \log_{10} L$. The estimates of the growth equation parameters were $W_\infty = 18.58$ kg and $K = 0.39$ yr^{-1}.

The length–weight relation for brown trout in Lake Michigan based on 312 observations in Wisconsin waters (Argonne National Laboratory, unpublished data) was $\log_{10} W = -4.46 + 2.86 \log_{10} L$. The growth rate and asymptotic weight were estimated as $K = 0.23$ yr^{-1} and $W_\infty = 7.76$ kg.

Estimates of PCB concentrations in the waters of Lake Michigan vary from 1 to 13 ng/L (Neely 1977). No estimate was available for Cayuga Lake; we used 10 ng/L for Green Bay, Lake Michigan, and Cayuga Lake.

Alewife is the principal food of larger lake trout and salmon in Lake Michigan. The PCB concentration of alewife in Lake Michigan averaged 3 mg/kg (Scheffy 1977). Alewife also are a large component in the diet of lake trout in Cayuga Lake (Carlander 1969). Measurements of PCB concentrations in alewife of Cayuga Lake have not been made, but concentrations of PCBs and DDT in other species suggests a value of from 1.5 to 2 mg/kg (Dr D. Lisk, Pesticide Residue Laboratory, Cornell University, personal communication). Lake trout feed mainly on alewife after reaching about 500–600 g in Lake Michigan (Wright 1968) and 437 g in Cayuga Lake (Carlander 1969).

Estimates of the parameters β, e_{ef}, q_{ox}, ξ, e_w, and e_f were obtained from Norstrom et al. (1976, Table 1). The value of the clearance parameter k of 0.238 given in the text by Norstrom et al. (1976) was used, and oxygen concentrations were obtained from Norstrom et al. (1976, Table 5). The value of the metabolic parameter was read from Fig. 3 of Norstrom et al. (1976), and the values of q_a and q_f are the same as in Norstrom et al. (1976). Parameter estimates are summarized in Table 1.

Sensitivity Analysis

Change in parameter values gives a range of different uptake patterns; change in the metabolic parameters are particularly important. If the exponent for weight of the low-routine metabolic rate γ is low, the uptake curve is asymptotic (Fig. 1A). An increase in γ increases the low-routine energy demand so food consumption and uptake of PCBs increase. The increasing part of the curve on the left occurs as growth and uptake come into equilibrium during the period of rapid growth. The increasing concentrations on the right when γ is high occur as the rate of growth decreases toward zero, and the asymptotic size is approached.

Increase in the coefficient of low-routine metabolism α also changes the pattern of uptake, but when γ is low, the change in PCB concentration with change in α is not large (Fig. 1B). If γ is high, however, an increase in α produces a large increase in uptake (Fig. 1C). The average among species for the value of α is a function of temperature and varies from about 209.5 J/wk at 7°C to 1047.5 J/wk at 25°C (Norstrom et al. 1976).

Change in α and γ impact on PCB concentrations of larger individuals because they relate to low-routine metabolism which is a function of body size. Change in β, which is the coefficient that relates the growth rate with the energy associated with growth, impacts on the initial portion of the uptake curve because β is a function of the growth rate, and the growth rate is higher for younger fish (Fig. 1D).

Change in the growth coefficient K from 0.10 yr^{-1} to 0.40 yr^{-1} does not change the shape of the uptake curve, but with $\gamma = 1.25$ increase in K results in a substantial increase in uptake (Fig. 1E). Growth rates for species vary considerably; for example, the growth rate for lake trout varies from 0.08 yr^{-1} in Kaminuriak Lake (Bond 1975) to 0.24 yr^{-1} in Cayuga Lake (Webster et al. 1960). A large difference in the growth rate could cause a large difference in uptake. Change in asymptotic weight has little effect on uptake (Fig. 1F).

The exposure parameters e_{pf}, C_f, e_{pw}, and C_w all enter the model in a similar way. For example, food concentrations of 5, 4, 3, 2, and 1 mg/kg are equivalent to e_{pf} values of 100, 80, 60, 40, and 20% with $C_f = 5$ mg/kg. Changes in the exposure parameters do not change the shape of the uptake curve but they do have a substantial effect on the level of the curve as is shown by changing the concentration of PCBs in the food (Fig. 1G).

The effect of the joule equivalent parameters q_f and q_a on the pattern of uptake is rather complex. The coefficient q_a influences the quantity of food necessary for growth, and q_f influences the quantity of food necessary for metabolism as well as growth. If $\gamma = 0.80$, and if the parameters for joule equivalents are equal, change in q_a and q_f have little effect on PCB uptake. However, if $\gamma = 0.80$ and the two coefficients are not equal, change in q_f and q_a can produce significant change in the rate of PCB uptake. For example, if $q_f = 6285$ J/g and $q_a = 8380$ J/g, the rate of uptake increases (Fig. 1H) because food consumption must increase to maintain the energy requirements for growth. If $q_f = 8380$ J/g and $q_a = 6285$ J/g, the rate of uptake decreases (Fig. 1H). When γ is low, changes in q_f and q_a do not change the shape of the uptake curve.

If γ is high, change in uptake with change in q_a and q_f is more complex. If q_a and q_f are equal, the rate of uptake decreases as q_f and q_a increase. When q_f is high, less food is required for metabolism and growth, but when q_a is high, more food is needed for growth. When γ is high, energy necessary for metabolism relative to energy necessary for growth increases, and an increase in q_f more than offsets a corresponding increase in q_a, and food intake and PCB accumulation decrease. If q_f and q_a are not equal, the pattern of the curve changes with change in q_f and q_a (Fig. 1I). If q_f is higher than q_a, food consumption is less than when q_f equals q_a and PCB uptake is less.

The model is not sensitive to increase in the clearance coefficient until the coefficient reaches about 0.01 g/wk, then further increase in k has a substantial effect on accumulation of PCBs (Fig. 1J). The clearance coefficient is an important parameter, but change in the clearance coefficient does not change the shape of the uptake curve.

Uptake by Different Species

For each species and each site there is considerable

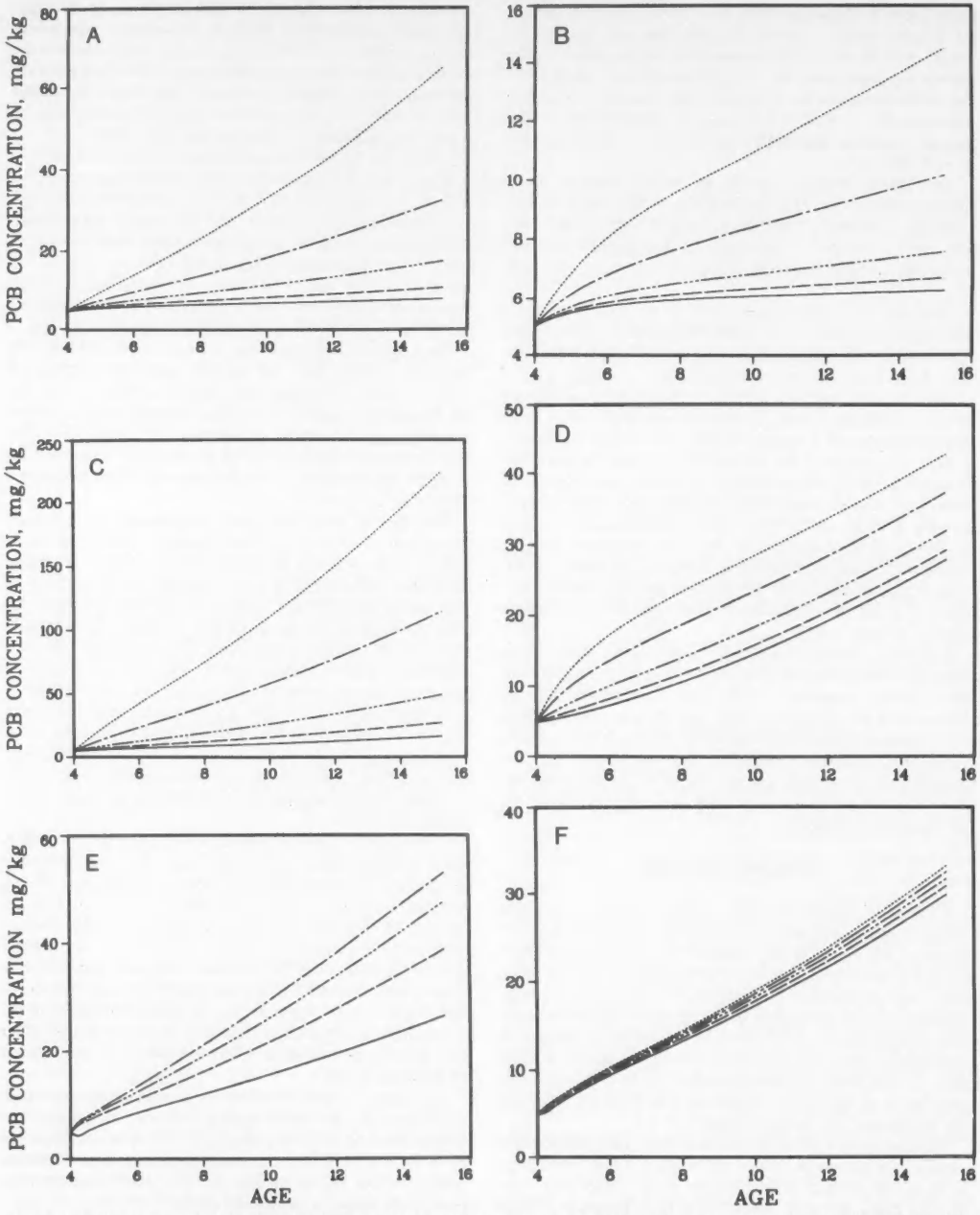

FIG. 1. (A) Change in uptake of PCBs with change in the metabolic parameter γ; from the top down γ = 1.3, 1.2, 1.1, 1.0, and 0.90. (B) Uptake of PCBs with change in the metabolic parameter α with γ at 0.80. From the top down α = 4190, 2095, 838, 419, and 209.5 J/wk. (C) Uptake of PCBs with change in the metabolic parameter α with γ at 1.25. From the top down α = 4190, 2095, 838, 419, and 209.5 J/wk. (D) Uptake of PCBs with change in the metabolic parameter β with γ = 1.20; from the top down β = 3, 2, 1, 0.5, and 0.25. (E) Uptake of PCBs with growth coefficients K from the top down of 0.40, 0.30, 0.20, and 0.10 yr^{-1} (γ = 1.25). (F) Uptake of PCBs with asymptotic weights from the top down to 5, 6, 7, 8, and 9 kg.

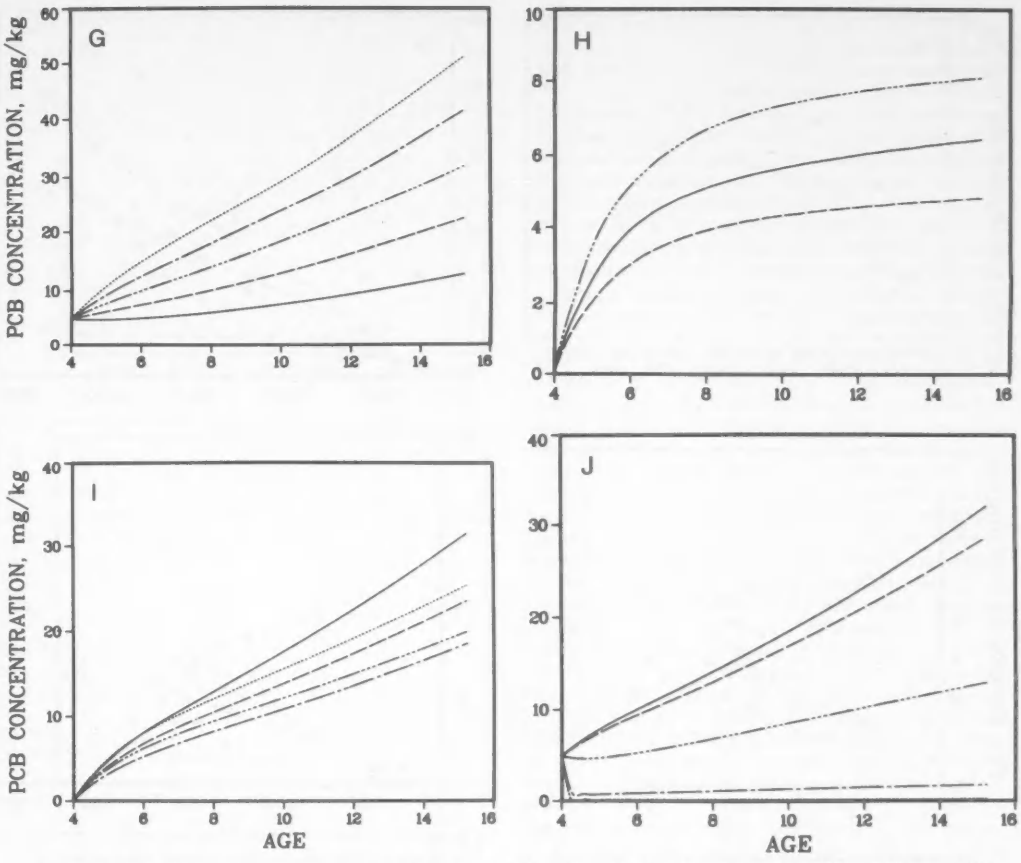

FIG. 1. (G) Uptake of PCBs with food concentration of PCBs at 5, 4, 3, 2, and 1 mg/kg from the top down ($\gamma = 1.25$). (H) Uptake of PCBs with $\gamma = 0.80$ and joule equivalents from the top down: $q_f = 6285$, $q_a = 8380$; $q_f = 8380$, $q_a = 8380$; $q_f = 8380$, $q_a = 6285$ J/g. If $q_a = q_f$ all curves fall close to the middle curve. (I) Uptake of PCBs with $\gamma = 1.20$ and joule equivalents from the top down: $q_f = 4190$, $q_a = 4190$; $q_f = 6285$, $q_a = 8380$; $q_f = 6285$, $q_a = 6285$; $q_f = 8380$, $q_a = 8380$; $q_f = 8380$, $q_a = 6285$. (J) Uptake of PCBs with the clearance coefficient at 0.0014, 0.01, 0.10, 1.0, and 10 $g^{-0.58} \cdot wk^{-1}$ from the top down.

variation in PCB concentration (Fig. 2A–I) and variation increases with weight. Despite wide scatter among the observations, there are trends in the data, and it is these trends which we hope to describe using a deterministic model for toxicant bioaccumulation. The fit of the model to the observed concentrations was examined as a function of weight as in Norstrom et al. (1976).

For brown trout there is an initial rapid increase of PCB concentration with size and then a lower increase with size at higher weights (Fig. 2A). Application of the model with the parameter estimates of Norstrom et al. (1976) describes the trend. The curve is nearly asymptotic and is similar to the curve obtained for PCB uptake by yellow perch (*Perca flavescens*) (Norstrom et al. 1976).

Application of the model to describe PCB uptake by lake trout in Lake Michigan using the parameter values estimated by Norstrom et al. (1976) gives low estimates; the predicted curve is not of the correct shape (Fig. 2B). The observed PCB concentrations for lake trout are not asymptotic; concentrations increase rapidly at larger weights. To fit the model the metabolic parameter γ was adjusted.

The model describes observed PCB uptake for lake trout only when γ is increased; the predictions fit trends in the observed PCB data with γ values of from 1.20 to 1.25. These values of γ are high, but the value of 0.80 applied by Norstrom et al. (1976) is too low. Paloheimo and Dickie (1966) state that under standard conditions γ is about 0.86, but in their review they found values of γ that ranged from 0.31 to 1.19. Glass (1969) reported the average γ for 26 different studies as 0.94 with a 95% confidence interval of 0.08. The γ values ranged from 0.62 to 1.31; 23% were greater than 1 and 15% were greater than 1.25.

The model could be fitted by increasing γ to about 0.95 and then increasing α as necessary. Although this approach gives values of γ that are closer to the average of values reported in the literature, it gives an α value that is too high, and hence

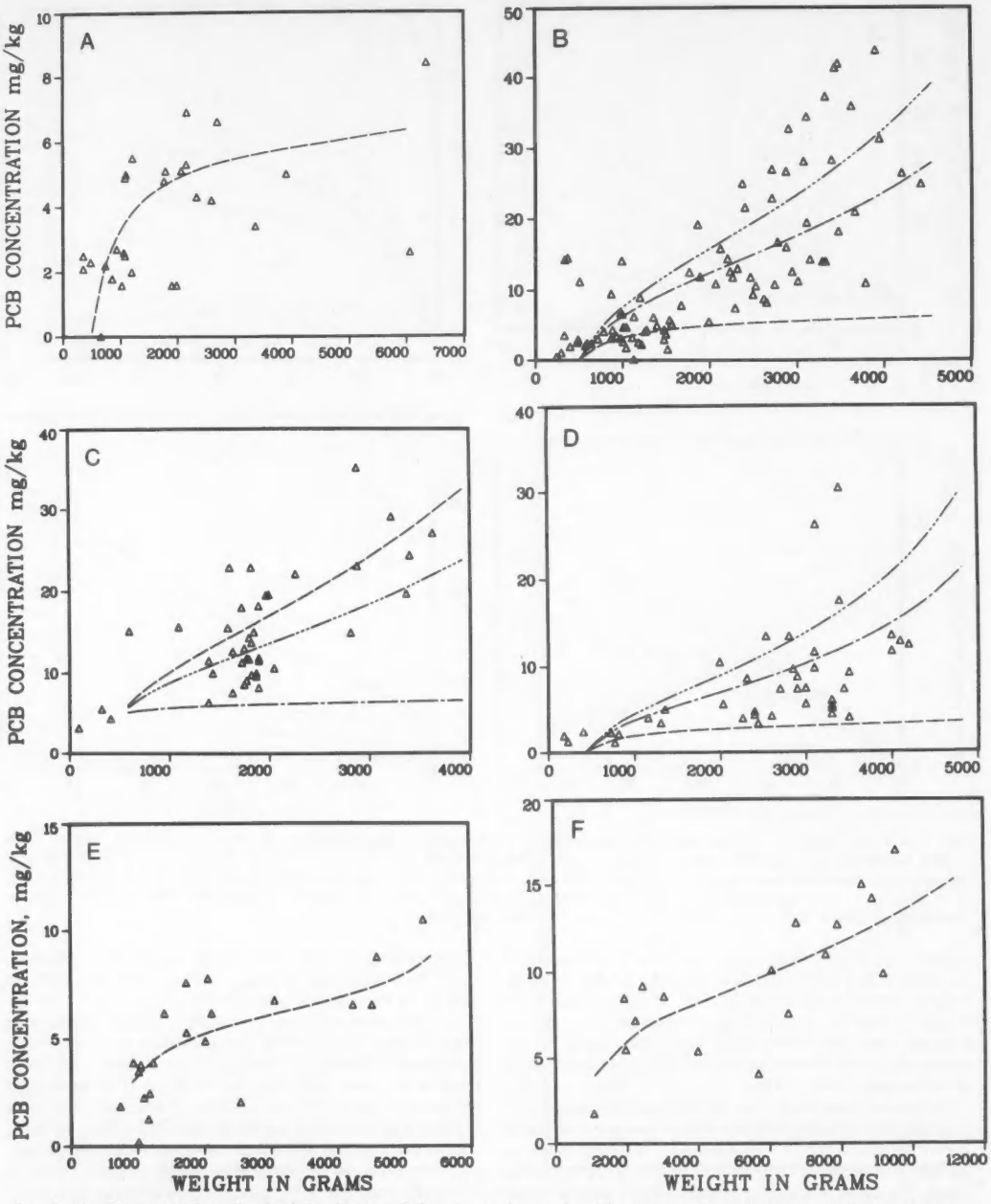

FIG. 2. (A) Observed and predicted relation between PCB concentrations and weight for brown trout (*Salmo trutta*) in Lake Michigan ($\gamma = 0.80$). (B) Observed and predicted PCB concentrations of lake trout (*Salvelinus namaycush*) from Lake Michigan. Top curve predictions with $\gamma = 1.25$, middle curve $\gamma = 1.20$, and bottom curve $\gamma = 0.80$. (C) Observed and predicted PCB concentrations of lake trout (*Salvelinus namaycush*) from Green Bay. Top curve predictions with $\gamma = 1.25$, middle curve $\gamma = 1.20$, and bottom curve $\gamma = 0.80$. (D) Observed and predicted relations between PCB concentrations and weight for Cayuga Lake lake trout (*Salvelinus namaycush*). Top curve $\gamma = 1.25$, middle curve $\gamma = 1.20$, and bottom curve $\gamma = 0.80$. (E) Observed and predicted PCB concentrations for coho salmon (*Oncorhynchus kisutch*) from Lake Michigan, $\gamma = 1.00$. (F) Observed and predicted concentrations for chinook salmon (*Oncorhynchus tshawytscha*) from Lake Michigan, $\gamma = 1.20$.

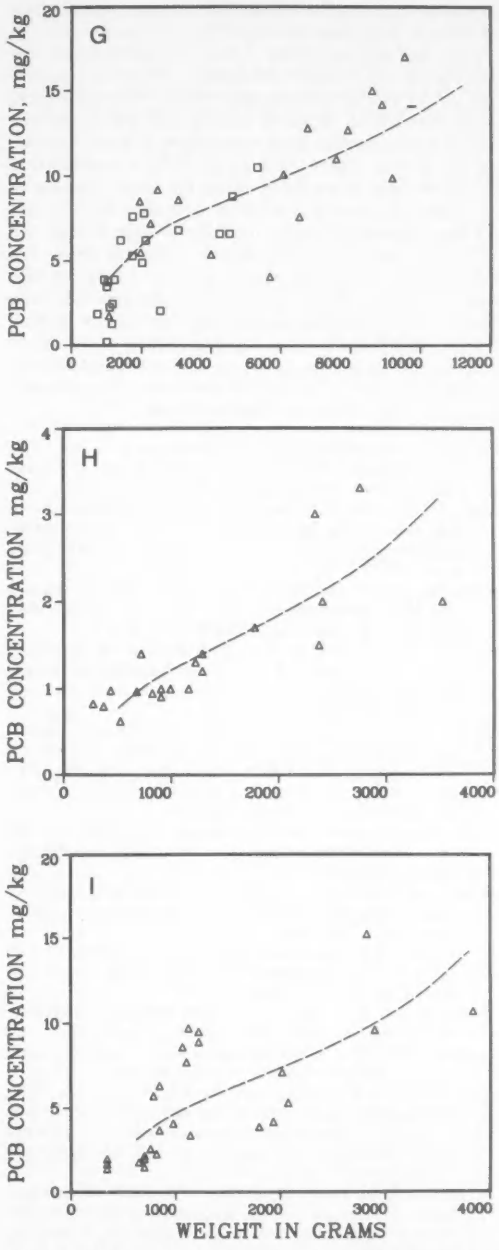

FIG. 2. (G) Observed and predicted PCB concentrations in coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*). Predictions were made with the model fitted to chinook growth data, $\gamma = 1.20$. (H) Observed and predicted PCB concentrations in lake whitefish (*Coregonus clupeaformis*) from Lake Michigan, $\gamma = 1.20$. (I) Observed and predicted PCB concentrations in lake whitefish (*Coregonus clupeaformis*) from Green Bay, $\gamma = 1.20$.

both α and γ are high.

The high value of γ necessary to fit the model probably results from an incomplete formulation of the model and a difference between the standard metabolic demands of fishes in the laboratory and the metabolic demands of fishes swimming about under natural conditions. In development of the model total metabolic demand was separated into standard, active, food utilization, and foraging metabolic demands. Nearly all laboratory studies have been done under standard conditions (Norstrom et al. 1976). Norstrom et al. (1976) assumed that both standard and active metabolism could be represented as $Q = \alpha W^{\gamma}$, and that γ was the same for both components. The energy demand of foraging was assumed zero (Norstrom et al.1976). The energy demand of reproduction is included in neither the expression for growth nor the expression for energy demand. We concluded that in the Norstrom et al. (1976) model, γ is not a measure of the exponent of weight under standard metabolic conditions, and we have defined γ as simply the exponent for metabolism rather than as the exponent for low-routine metabolism as in Norstrom et al. (1976). Given the paucity of metabolic data a reasonable method for estimation of γ is to fit the model to one data set by variation of γ and then examine the fit to other data sets. Simulation with a γ value of 1.25 gave a good fit of predictions to the trend in the observed PCB data for lake trout in Lake Michigan, and so this value was applied.

The model fitted to data for lake trout in Lake Michigan was applied without adjustment of parameters to predict the PCB concentrations of lake trout in Green Bay. The predictions fit the trend in the observations (Fig. 2C). The asymptotic weight for Green Bay could not be estimated so the value for Lake Michigan was used. Decreasing the asymptotic weight of lake trout in Green Bay to locate the inflection of the growth curve closer to the weight where PCB concentrations begin to increase improves the fit of the predicted PCB concentrations to the observed values. The asymptotic weight in Green Bay may be lower than in Lake Michigan. Simulations indicate that the observed differences in PCB concentrations between lake trout from Green Bay and Lake Michigan result from differences in size.

The model also was applied without changing parameter values, except those as estimated for growth and food concentration, to predict uptake of PCBs by lake trout in Cayuga Lake. The pattern of uptake by lake trout is similar in Lake Michigan, Green Bay, and Cayuga Lake, and the predictions for Cayuga Lake fall well within the natural scatter of the data (Fig. 2D). Simulation indicates that PCB concentrations in lake trout of Cayuga Lake are lower than those in Lake Michigan and Green Bay because the PCB concentration in the food of Cayuga Lake lake trout is lower.

A good fit to the trend in the coho data is obtained with $\gamma = 1.0$ (Fig. 2E). For chinook salmon the model describes the trend with $\gamma = 1.20$ (Fig. 2F), and when the data for coho and chinook are combined they fall along the same trend and the model for chinook works equally as well for coho as for chinook (Fig. 2G). This suggests that the asymptotic weight for coho salmon was underestimated.

Simulation indicates that PCB concentrations in chinook are higher than concentrations in coho because coho are exposed for a shorter period of time and attain smaller sizes than chinook. In Lake Michigan both coho and chinook spawn in the fall and smolt or are stocked the following spring. Coho spend about 18 mo in the lake before returning to spawn.

Chinook spend an additional year in the lake where they continue to grow and accumulate PCBs. Lake trout have higher concentrations of PCBs than salmon because they grow slower and live longer than salmon and are exposed to PCBs for a longer time.

Most research on food chain uptake of microcontaminants by fish has focused on uptake by piscivores. Lake whitefish feed largely on aquatic insect larvae, mollusks, and amphipods; yet in Green Bay lake whitefish accumulate high concentrations of PCBs. The PCB concentrations in food of lake whitefish, to our knowledge, have not been determined; therefore, the model was applied by adjusting the concentration of PCBs in the food until a good fit to the trend in the data was obtained. In Lake Michigan the PCB concentrations in lake whitefish are low (Fig. 2H) and follow the characteristic pattern of an initial rapid increase followed by a leveling off and then another increase.

The trend in the Lake Michigan data is described by the model with a food concentration of 0.30 mg/kg and $\gamma = 1.20$. PCB concentrations in lake whitefish from Green Bay are considerably higher than those from Lake Michigan, and the pattern is less distinct. This is partly the result of a lack of data for larger fish in Green Bay, but the variability in Green Bay is higher too. The model describes the trend in the Green Bay data with a food concentration of 2.1 mg/kg and $\gamma = 1.20$ (Fig. 2I).

After correction for differences in size there is no difference in PCB concentration in lake trout between Lake Michigan and Green Bay, but a large difference occurs in lake whitefish. This difference in uptake between lake trout and lake whitefish may result from differences in their food chain relations. Lake trout are terminal carnivores in the food chain: phytoplankton−zooplankton−alewife−lake trout. In this food chain PCB uptake is from the water, and the PCB concentrations in the water are likely to be rather uniform over wide areas. Lake whitefish are terminal carnivores in the food chain: detritus−bottom fauna−lake whitefish. In this food chain PCB uptake is from the bottom sediments as well as from the water, and there may be variation in contamination among different areas.

Simulation indicates there are some differences in the proportions of PCBs accumulated from the water. Lake trout in Green Bay and Lake Michigan and salmon and brown trout in Lake Michigan accumulate about 7.5% of their PCB body burdens from the water. Lake whitefish accumulate about 10% of their PCBs from the water in Green Bay and 42% from the water in Lake Michigan. These differences result from variation in the PCB concentrations in their foods. A higher food concentration results in a larger proportion of uptake from food.

Asymptotic uptake of contaminants often has been reported (Branson et al. 1975; Elwood and Eyman 1976; Hamelink 1977; Norstrom et al. 1976; Thomann 1981). In laboratory studies an apparent equilibrium often is observed, but the tests are short term and done with small, rapidly growing fish. The bioenergetic model indicates that uptake will appear asymptotic under these conditions. Equilibrium is predicted by compartment models that ignore growth (Hamelink 1977; Nealy 1977) and by models that apply the exponential model to describe growth (Thomann 1981). The exponential model is suitable for small, rapidly growing fish or for modeling growth of larger fish for awhile, but it does not describe fish growth over a life span (Ricker 1979).

Field data and application of the bioenergetic model both indicate that when uptake is examined over the life span of a fish, uptake may not be asymptotic. For all species examined, except brown trout, uptake was at first rapid and then slowed toward a plateau before again beginning to increase. In younger fish the rate of growth is high and PCBs accumulated are diluted by rapid accumulation of new fish tissue. There is an inflection in the growth in weight curve at about 0.3 W_∞, and the rate of growth begins to slow. If γ is large enough, the PCB concentration begins to increase as growth slows. The inflections of the growth curves occur at 1.8 kg for lake whitefish in Lake Michigan, 1.78 kg for lake trout in Cayuga Lake, 1.58 kg for coho salmon, and 5.57 kg for chinook salmon. PCB concentrations begin to increase at the inflection points of the growth curves in every case except for coho salmon (Fig. 2A−I), and as indicated earlier the asymptotic weight of coho salmon is an underestimate.

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A Quantitative Study of Economically Important Parasites of Walleye Pollock (*Theragra chalcogramma*) from British Columbian Waters and Effects of Postmortem Handling on Their Abundance in the Musculature

J. R. ARTHUR, L. MARGOLIS, D. J. WHITAKER, AND T. E. MCDONALD

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

ARTHUR, J. R., L. MARGOLIS, D. J. WHITAKER, AND T. E. MCDONALD. 1982. A quantitative study of economically important parasites of walleye pollock (*Theragra chalcogramma*) from British Columbian waters and effects of postmortem handling on their abundance in the musculature. Can. J. Fish. Aquat. Sci. 39: 710–726.

The identity of parasites infecting the musculature and body cavity (including external surfaces of viscera) of walleye pollock (*Theragra chalcogramma*) collected from two British Columbian localities, their distribution within the host's musculature, and the influence of host sex, length, and method of postmortem handling on parasite prevalence and abundance were determined. Three parasite species were found only in the musculature (*Pleistophora* sp., pseudophyllidean plerocercoids, and *Phocanema decipiens* (Krabbe, 1878) larva), two species only in the body cavity (*Contracaecum*-type larva and *Hysterothylacium aduncum* (Rudolphi, 1802) larva), and two species in both sites (*Anisakis simplex* (Rudolphi, 1809) larva and *Nybelinia surmenicola* Okada in Dollfus, 1929 plerocercoid). In the musculature most *A. simplex* and *N. surmenicola* infected the region surrounding the body cavity, with *A. simplex* being distributed more anteriorly, while most pseudophyllidean plerocercoids occurred in the caudal region. No preferred site of infection was observed for *P. decipiens* larvae. No statistically significant differences in infection with any of these helminths occurred between right and left body musculature. For pollock of similar lengths, males were more heavily infected than females with larvae of *A. simplex* and plerocercoids of *N. surmenicola*. Three species (*A. simplex*, *N. surmenicola*, and *Pleistophora* sp.) occurred with greater prevalence or abundance in larger fish. Storage of eviscerated and round pollock from the Strait of Georgia on ice at 3°C for periods of up to 7 d did not result in any significant change in the prevalence of infection or abundance of parasites in the musculature. The abundance of these parasites in pollock from Queen Charlotte Sound, northern British Columbia, appears similar to that previously reported for some other areas of the North Pacific Ocean (although not as high as the most heavily infected stocks of the northwest Pacific) while their abundance in fish from the Strait of Georgia, southern British Columbia, appears to be the lowest for any pollock stock examined.

Key words: walleye pollock, *Theragra chalcogramma*; economically important parasites, *Pleistophora* sp., pseudophyllidean plerocercoids, *Nybelinia surmenicola* plerocercoid, *Phocanema decipiens* larva, *Contracaecum*-type larva, *Hysterothylacium aduncum* larva, *Anisakis simplex* larva, British Columbia

ARTHUR, J. R., L. MARGOLIS, D. J. WHITAKER, AND T. E. MCDONALD. 1982. A quantitative study of economically important parasites of walleye pollock (*Theragra chalcogramma*) from British Columbian waters and effects of postmortem handling on their abundance in the musculature. Can. J. Fish. Aquat. Sci. 39: 710–726.

Nous avons identifié les parasites infestant la musculature et la cavité du corps (y compris les faces externes des viscères) de morues du Pacifique occidental (*Theragra chalcogramma*) capturées en deux endroits de la Colombie-Britannique. Nous avons de plus déterminé la distribution de ces parasites dans la musculature de l'hôte, ainsi que l'influence du sexe, de la longueur et de la méthode de manipulation post-mortem de l'hôte sur la prédominance et l'abondance des parasites. Seulement trois espèces parasites ont été trouvées dans la musculature (*Pleistophora* sp., plérocercoïdes pseudophyllidiens et larve de *Phocanema decipiens* (Krabbe, 1878)), seulement deux espèces dans la cavité du corps (larve de type *Contracaecum* et larve d'*Hysterothylacium aduncum* (Rudolphi, 1802)) et deux espèces à l'un et l'autre site (larve d'*Anisakis simplex* (Rudolphi, 1809) et plérocercoïde de *Nybelinia surmenicola* Okada dans Dollfus, 1929). Dans la musculature, la plupart des *A. simplex* et

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N. surmenicola infestent la région entourant la cavité du corps, *A. simplex* étant réparti plus en avant, alors que les pleurocercoïdes pseudophyllidiens se trouvent dans la région caudale. Les larves de *P. decipiens* ne semblent pas avoir de site d'infestation préféré. Nous n'avons pas observé de différences significatives à l'analyse statistique dans l'infestation de la musculature droite et gauche du corps par l'un ou l'autre des trois helminthes. À longueur corporelle égale, les mâles sont plus lourdement infestés que les femelles par les larves de *A. simplex* et les plérocercoïdes de *N. surmenicola*. Trois espèces (*A. simplex*, *N. surmenicola* et *Pleistophora* sp.) prédominent plus fréquemment ou se trouvent en plus grande abondance chez les grands poissons. L'entreposage de la morue du Pacifique occidental en provenance du détroit de Géorgie, à l'état éviscéré et rond, sur de la glace à 3°C pendant des périodes allant jusqu'à 7 jours ne modifie pas de façon significative la prédominance de l'infestation ou l'abondance des parasites dans la musculature. L'abondance de ces parasites chez cette espèce capturée bassin Reine-Charlotte, dans le nord de la Colombie-Britannique, semble identique à celle déjà signalée dans d'autres régions du Pacifique nord (bien qu'elle ne soit pas aussi élevée que dans les stocks les plus lourdement infestés dans le Pacifique nord-ouest). Par ailleurs, l'abondance de ces parasites chez des morues du détroit de Géorgie, dans le sud de la Colombie-Britannique, semble la plus faible de tous les stocks de morues du Pacifique occidental examinés.

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THE walleye pollock (*Theragra chalcogramma*), one of the most abundant fishes of the North Pacific Ocean and Bering Sea, has only in recent years gained great economic importance as a food fish. Although pollock have long been taken in large numbers by the Japanese and Korean fisheries, no extensive Soviet or North American fishery existed until approximately 1960. Soviet fishery industries until that time utilized incidental catches of pollock primarily in the production of fertilizer and as food for fur-bearing mammals, the musculature being considered unsuitable for human consumption because of the low aesthetic appeal of fillets infected with pleroceroids of the cestode *Nybelinia surmenicola* Okada in Dollfus, 1929 (see Oshmarin et al. 1961; Mamaev and Baeva 1963; Mamaev 1965). Additional concern has frequently been raised by Japanese and Soviet workers over the low quality of pollock musculature infected with microsporidan cysts (presumably *Pleistophora* sp.) and the infection of the musculature and/or viscera by larval anisakid nematodes (*Anisakis simplex* (Rudolphi, 1809), *Phocanema decipiens* (Krabbe, 1878), and *Contracaecum*-type larva) and plerocercoids of the cestode *Pyramicocephalus phocarum* (Fabricius, 1780), all of which are aesthetically objectionable or of significance as potential human pathogens (see Mamaev and Baeva 1963; Sasaki 1973; Suzuki and Oishi 1974). Although discarding heavily infected fish and the development of processing methods that remove the most heavily infected portions of the musculature have allowed pollock to become one of the most valuable fishery resources of the Soviet Union and Japan, infection by parasitic helminths and Microsporida remains a serious problem (Mamaev and Baeva 1963; Mamaev et al. 1965; Kazykhanov and Slipchenko 1970; Sasaki 1973). For example, Kazykhanov and Slipchenko (1970) estimated that about 10% of pollock examined from Sakhalin were unsuitable for human consumption under Soviet health regulations because of infection by *N. surmenicola*. Based on examination of pollock exported to Poland from the Soviet Union, Grabda (1977) concluded that the species was poorly suited for the Polish import market as a result of the low quality of heavily infected fish and the need for additional inspection.

Stocks of walleye pollock occurring in Canadian waters have not yet been heavily exploited. Although pollock now account for as much as 10.6% of the total Canadian groundfish landings from the Pacific Ocean (Thompson 1981), they were, until recently, used almost exclusively in the manufacture of food for fur-bearing animals (Forrester 1958). Only since 1976 have catches of Canadian pollock been processed in quantity for human consumption, with exports going primarily to the United States. In addition an experimental fishery for pollock roe, which is considered a delicacy in Japan, has greatly increased the value of Canadian landings since 1978. It is likely, therefore, that pollock will continue to gain in importance as a Canadian fishery resource as demand increases for the export of both pollock fillets and roe.

Parasitic infection of the musculature of walleye pollock from British Columbian waters may, at times, present a problem for the fishing industry (D. D. Wilson, Department of Fisheries and Oceans, Vancouver, B.C., personal communication). The present study was undertaken to investigate the prevalence and abundance of parasites occurring in the musculature and body cavity of pollock from two localities in British Columbian waters, their identity, and distribution within the host's musculature. The influence of host sex (for fish of equal length) and host length (age), and method of postmortem handling of the fish, on prevalence and abundance of the parasites were also examined. Many previous studies have shown that the level of parasitic infection of marine fishes is associated with these variables (see, for example, Bishop and Margolis 1955; Platt 1975; Smith and Wootten 1975).

Materials and Methods

Primary collections of walleye pollock were obtained from Porlier Pass (49°N, 123°35′W), Strait of Georgia, British Columbia (Fig. 1) in December 1972 (Table 1). These collections were designed to investigate the possible effects of different handling methods after capture in determining the

prevalence, abundance,[1] and distribution of parasites in the musculature of walleye pollock and to investigate the role played by host length in determining the prevalence and abundance of infection of the musculature and body cavity (including the external visceral surfaces). Collections of pollock from southeast Goose Island Grounds (51°25′N, 129°10′W), Queen Charlotte Sound, taken in September 1978 were also analyzed to provide additional information on the distribution of helminths in the musculature of pollock and on the importance of host length in determining the prevalence and intensity of parasitism (Table 1).

Treatment of Collections

Storage time on ice — To determine if a relationship exists between storage time on ice and the prevalence and abundance of parasites in the musculature of pollock, size-selected fish collected at Porlier Pass were divided into six groups of 25 fish each and of approximately equal size composition. Four of these collections were maintained as round fish and were stored on ice in a cold room at ~3°C for periods of 0, 1, 3, or 7 d. The remaining two samples of 25 pollock each were eviscerated immediately after capture and then stored on ice for periods of 3 and 7 d. After storage on ice all collections were either quick-frozen to −40°C on a plate freezer on board ship or were frozen on shore to −30°C in a chest freezer.

Effects of host length — For investigation of the possible role of host length, additional samples of small- and large-sized fish were collected from Porlier Pass and deep-frozen immediately after capture. Collections of male and female pollock from Queen Charlotte Sound used in these analyses were similarly deep-frozen as round fish. Because preliminary investigation revealed that prevalence and abundance of parasites of the musculature and body cavity of pollock were not affected by storage on ice but were significantly related to host sex (at a given length), collections of male and female fish were analyzed separately and were reorganized to utilize data from all pollock for which both the musculature and body cavity were examined. For comparison, male and female fish from each locality were divided into three length categories (small, medium, large) such that categories to be compared contained equal numbers of hosts (Table 1). To obtain equal sample sizes, the minimum and maximum lengths of successive categories frequently were required to be identical. In such instances assignment of individual fish of these common lengths to one or other of the successive categories was made randomly. Data on parasites occurring in the musculature were analyzed separately and then combined with data from the body cavity for examination of collections based on total numbers for each species.

Host Necropsies

Hosts frozen in the round were thawed in the laboratory; total length (cm), weight (g), and sex taken; the viscera removed; and the body cavity rinsed and examined for any parasites adhering to the peritoneum. The viscera were then examined for parasites free or encysted on the external surface or mesenteries and, for hosts examined from Queen Charlotte Sound, the esophagus and stomach were split open, the contents removed, and the wall pressed between two Plexiglas plates and examined for encysted parasites under a dissecting microscope. The body musculature of all pollock was cut from the vertebral column and the skin removed from the fillets. The flesh was then sliced in thin transverse sections and the number and position of any parasites observed was recorded.

Parasites recovered were treated using standard parasitological techniques and identified to species where possible. Representative material is retained in the parasitological collection of the Pacific Biological Station.

Statistical Methods

To express the parasite data quantitatively we used raw numbers of parasites, including zero, in each host, and the concepts denoted by the terms *prevalence*, *intensity*, and *abundance*, defined as follows (Margolis et al. 1982):

Prevalence = Number of hosts infected ÷ Number of hosts examined (usually expressed as a percentage).

Intensity = Numbers of parasites in each infected host (usually expressed as a range).

Abundance = Total number of parasites in a sample of hosts ÷ Number of hosts examined (infected + uninfected) = Mean number of parasites per host examined.

We have chosen to use *abundance* rather than *mean intensity* (mean number of parasites per *infected* host in a sample) because data from infected and uninfected fish were included in all statistical analyses.

Because the distribution of raw parasite numbers was obviously nonnormal, nonparametric methods of analysis were used throughout the study. Where parasite prevalence and parasite numbers of two samples were compared, the Mann−Whitney U-test was used; for similar analyses involving three or more collections, the Kruskal−Wallis test was used (see Sokal and Rohlf 1969). Sets of collections showing significant heterogeneity were further analyzed by comparison of all combinations of pairs using the nonparametric simultaneous test procedure (STP) as described in Sokal and Rohlf (1969).

Results

Comments on Species of Parasites Recovered

The following comments are included to provide brief background information on the seven species of parasites encountered during this study.

Pleistophora sp. — A protozoan (microsporidan) parasite producing small, spindle-shaped, whitish cysts in the musculature was recorded from 30.1% of the walleye pollock examined from Queen Charlotte Sound in 1978. This species has apparently been reported from pollock from Canadian waters by Hoskins and Hulstein (1977) as an unidentified species of Microsporida, and was tentatively identified as *Glugea punctifera* Thélohan, 1895 by Kingsbury (1978) in pollock from

[1]See subsection on Statistical Methods for definitions of prevalence, intensity, and abundance.

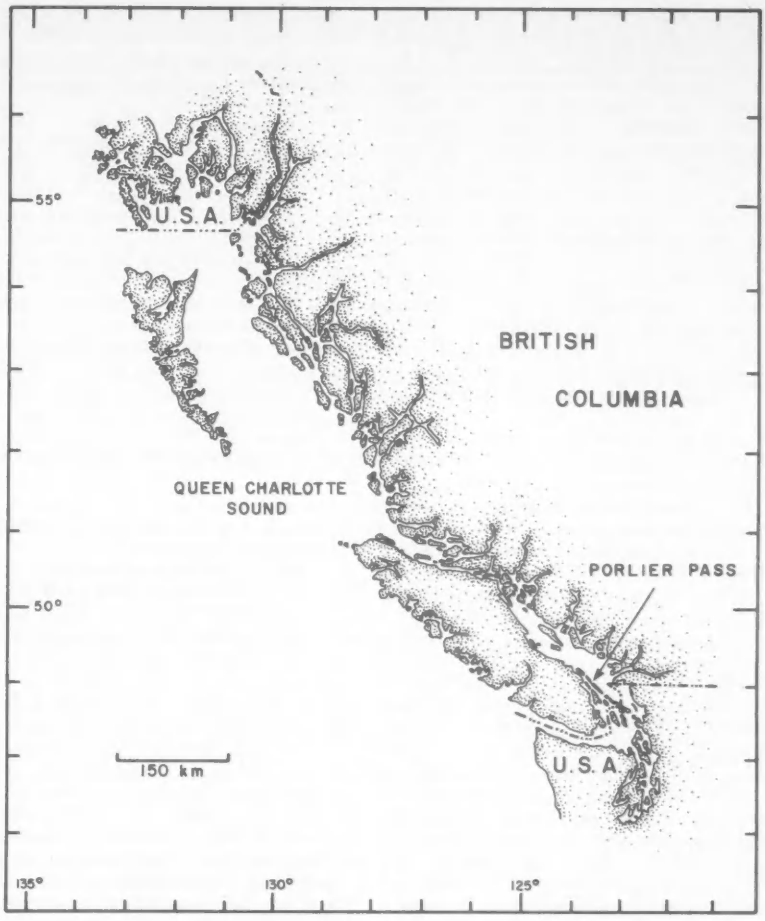

FIG. 1. Coastal British Columbia showing collection localities — Porlier Pass and Queen Charlotte Sound.

Alaska. It has also been reported as *G. punctifera* from pollock from the northwestern Pacific Ocean by Akhmerov (1951) and Sasaki (1973) and as unidentified Microsporida by Grabda (1977).

Although the specific identity of our material from Canadian walleye pollock has not been determined, it does not appear to be conspecific with *G. punctifera*, a species originally described from the musculature of the eye of *Pollachius pollachius* from the northwestern Atlantic Ocean. Although *Pleistophora* sp. was not recorded in pollock from Porlier Pass examined during this study, it is widely distributed in British Columbian waters and has been observed in fish taken from Swanson Channel (J. R. Arthur unpublished data), an area of the Strait of Georgia not far from Porlier Pass.

Nybelinia surmenicola Okada in Dollfus, 1929, plerocercoid — This juvenile cestode is a common parasite of the body cavity and musculature of marine fishes in Canadian Pacific waters (Margolis and Arthur 1979) and has previously been reported from Canadian walleye pollock by Wardle (1933) and Arai (1967, 1969). Pollock examined from Queen Charlotte Sound during this study were highly infected with *N. surmenicola* (prevalence, 70.2%; intensity, 1–678) whereas those from Porlier Pass were only occasionally infected (prevalence, 8.3%; intensity, 1–13). Numerous reports of *N. surmenicola* from *T. chalcogramma* from the northwestern Pacific Ocean have been made by Japanese and Russian workers (see, for example, Zhukov 1960; Skrjabina 1963; Sasaki 1973).

Pseudophyllidea gen. sp. plerocercoid — Because of the immaturity of these diphyllobothriid-like plerocercoids found encysted in the caudal musculature of walleye pollock from

TABLE 1. Summary of collections of walleye pollock (*Theragra chalcogramma*). (Collections 1–3 are from Porlier Pass, Strait of Georgia, taken December 6–7, 1972, and collection 4 is from S.E. Goose Is. Grounds, Queen Charlotte Sound, taken September 23–24, 1978.)

No.	Treatment		Males, length (cm)			Females, length (cm)		
			N	$\bar{x} \pm$ SD	(range)	*N*	$\bar{x} \pm$ SD	(range)
1.	Iced (3°C) as round fish	0 d	19	37.2±1.8	(33–40)	6	39.7±0.9	(38–41)
		1 d	16	36.4±1.8	(34–40)	7	38.3±1.6	(35–40)
		3 d	18	36.3±2.1	(33–41)	6	38.3±2.5	(33–40)
		7 d	18	36.7±2.4	(33–41)	6	38.2±0.9	(37–39)
2.	Iced (3°C) as gutted fish	3 d	Unsexed *N* = 25			Length = 39.9±2.3		(36–44)
		7 d	Unsexed *N* = 25			Length = 40.4±2.2		(36–45)
3.	Combined collections: all round fish[a]	Small	28	29.7±4.1	(23–35)	16	29.8±5.4	(23–38)
		Medium	28	35.9±0.7	(35–37)	16	39.1±0.8	(38–40)
		Large	28	38.8±1.2	(37–41)	16	49.0±4.2	(40–56)
4.	Frozen immediately as round fish	Small	20	42.2±2.0	(39–45)	31	48.3±4.5	(36–53)
		Medium	20	47.6±1.4	(45–50)	31	58.5±2.2	(54–61)
		Large	20	55.8±5.7	(50–72)	31	65.3±3.5	(61–73)

[a]Includes all round fish iced for various periods plus additional round fish frozen immediately after capture.

TABLE 2. Results of the Mann–Whitney U-test for comparison of prevalence and abundance of parasites in collections of male and female walleye pollock of equal length composition from Queen Charlotte Sound. (Length: ♂ = ♀ = 50.4 ± 6.6 cm.) (*Indicates significant ($P < 0.05$) differences between collections.)

	Prevalence			Abundance (intensity range)		
	♂	♀	T_s	♂	♀	T_s
Pleistophora sp.	8/28	6/28	0.612	—	—	—
Nybelinia surmenicola plerocercoid	24/28	19/28	1.567	14.0 (1–186)	7.3 (1–56)	2.053*
Anisakis simplex larva	28/28	28/28	0.000	33.8 (2–108)	23.1 (6–77)	2.017*
Contracaecum-type larva	5/28	4/28	0.361	0.5 (1–3)	0.2 (1–3)	0.398
Phocanema decipiens larva	4/28	2/28	0.856	0.1 (1)	0.1 (1)	0.856

Porlier Pass (prevalence, 10.6%; intensity, 1–5), further identification was not possible. This species was not detected in pollock from Queen Charlotte Sound.

Anisakis simplex (Rudolphi, 1809) larva — This larval nematode is one of the most ubiquitous parasites of marine fishes of the northern hemisphere and has frequently been reported (as *Anisakis* sp. or *Anisakis*-type I larva) from *T. chalcogramma* caught off Japan and the U.S.S.R. (see, for example, Zhukov 1960; Skrjabina 1963; Koyama et al. 1969; Oishi and Hiraoki 1971; Grabda 1977). *Anisakis simplex* was found encapsulated or free in the mesenteries, on the viscera, in the body cavity, and in the musculature of walleye pollock, being more common in fish from Queen Charlotte Sound (prevalence, 99.0%; intensity, 2–269) than in those from Porlier Pass (prevalence, 66.7%; intensity, 1–19).

Contracaecum-type B larva — Larval nematodes identifiable as *Contracaecum*-type B larva of Koyama et al. (1969) were found encapsulated on the viscera and on the mesenteries of 20.9% of all pollock examined from Queen Charlotte Sound with an intensity of one to seven helminths per host. Although absent from fish collected at Porlier Pass, this species has been found with low prevalence in pollock from an adjacent stock at Swanson Channel (J. R. Arthur unpublished data). Previous records of this nematode from *T. chalcogramma* are those of Koyama et al. (1969), Sasaki (1973), and Suzuki and Oishi (1974), all from Japanese waters.

Contracaecum-type larvae from walleye pollock are morphologically similar to third-stage larvae of *Contracaecum osculatum* (Rudolphi, 1802) recently described by Valter (1979) from fishes of the White Sea. Adult *C. osculatum* often have been reported from pinnipeds from the eastern Pacific Ocean (Margolis and Dailey 1972). However, as other species of *Contracaecum* (as well as *Phocascaris*, whose larvae are generically indistinguishable from those of *Contracaecum*) may occur in British Columbian waters, the conspecificity of *Contracaecum*-type B larva from walleye pollock and *C. osculatum* must await further study.

Hysterothylacium (=*Thynnascaris*) *aduncum* (Rudolphi, 1802) larva — Larval *H. aduncum* are common nematode parasites of the viscera of marine fishes of the North Pacific Ocean (Margolis and Arthur 1979) and have previously been reported from *T. chalcogramma* from the U.S.S.R. by Grabda (1977). *Hysterothylacium aduncum*, both encapsulated on the viscera as a larva and free in the stomach and intestine as an adult, is a common parasite of walleye pollock in British Columbian waters. Larval *H. aduncum* were recorded from 67.0% (intensity, 1–23) of all pollock examined

from Porlier Pass and 43.8% (intensity 1–37) of those examined from Queen Charlotte Sound. It is likely that previous reports of larvae of this species from Canadian pollock are masquerading under records of *Contracaecum* sp. larva (see Arai 1967, 1969).

Phocanema decipiens (Krabbe, 1878) larva — This nematode species has frequently been reported from the musculature of marine fishes of the North Pacific Ocean (Margolis and Arthur 1979) and has been previously recorded as *Porrocaecum* sp. from Canadian walleye pollock by Arai (1969). In the present study it was found with relatively low prevalence (6.1 and 15.0%) and intensity (one to eight helminths per host) in both stocks examined. Other records of *P. decipiens* (as *Terranova d.*, *Terranova* sp., and *Porrocaecum* sp.) from *T. chalcogramma* include those of Koyama et al. (1969) and Shiraki (1974) from Japan, and Gusev et al. (1959), Strelkov (1960), Zhukov (1960), Mamaev and Baeva (1963), Skrjabina (1963), and Grabda (1977) from the U.S.S.R.

Comparison of Male and Female Pollock of Equal Length

To determine whether male and female pollock of the same length class could be combined for subsequent analyses, a preliminary analysis comparing the prevalence and abundance of parasites occurring in the musculature and body cavity of male and female walleye pollock of equal length composition was conducted on fish from Queen Charlotte Sound (Table 2). Comparisons of parasite prevalence using the Mann–Whitney U-test did not reveal any significant differences between male and female pollock of equal length for any of the five species of parasites examined. Similar comparisons using parasite numbers showed significant differences between collections for two of four species, *N. surmenicola* and *A. simplex*. Abundance of both *N. surmenicola* (14.0 vs. 7.3) and *A. simplex* (33.8 vs. 23.1) was higher in male than in female pollock from Queen Charlotte Sound (Table 2).

Because host sex was shown to be a significant factor in determining the numbers of parasites infecting walleye pollock of a given length class, collections of male and female fish were treated separately in all subsequent analyses.

Effect of Host Length

The role of host age, as reflected by length, in determining the prevalence of infection and numbers of parasites in the body cavity and musculature of pollock was investigated for male and female pollock from Porlier Pass and Queen Charlotte Sound.

Porlier Pass — Comparison of small-, medium-, and large-sized male pollock from Porlier Pass using the Kruskal–Wallis test showed significant heterogeneity among collections for prevalence and numbers only of *A. simplex* larvae infecting the musculature (Table 3). Pairwise comparison of collections did not, however, reveal any significant differences.

Similar analyses of female pollock from Porlier Pass revealed no significant heterogeneity among size groups for parasites of the musculature (Table 4). Comparison of collections using total parasite data showed significant interclass heterogeneity for both prevalence and numbers of *A. simplex* and *N. surmenicola*. Subsequent STP comparison of collections using prevalence of *A. simplex* showed small female pollock (5/16 infected) to differ significantly from both medium and large pollock (13/16 and 16/16 infected, respectively). Medium- and large-sized pollock were not different from each other. All pairwise comparisons of collections based on numbers of *A. simplex* gave significant results. Comparison of prevalence of total *N. surmenicola* in different size groups revealed that large female pollock (8/16 infected) differed from both small- and medium-sized fish (both with 0/16 infected). Comparison of numbers of *N. surmenicola* gave similar results (Table 4). Abundance of both *A. simplex* and *N. surmenicola* in female pollock increased with host size, with 0.6, 2.0, and 8.3 *A. simplex* and 0, 0, and 1.8 *N. surmenicola* recovered from small-, medium-, and large-sized female pollock, respectively (Table 4).

Queen Charlotte Sound — Comparisons of prevalence of infection in male pollock from Queen Charlotte Sound revealed significant heterogeneity among collections for *Pleistophora* sp. and total *N. surmenicola* (Table 5). Subsequent pairwise comparison of collections using prevalence of microsporidan cysts revealed no significant differences between pairs. However, examination of prevalence values showed a trend toward higher prevalence of *Pleistophora* sp. with increasing length, with 1/20, 6/20, and 8/20 hosts infected for small-, medium-, and large-sized fish, respectively. STP analysis of prevalence of *N. surmenicola* in collections of male pollock showed small pollock (6/20 infected) to differ from both medium- and large-sized fish (17/20 and 20/20 infected, respectively). Analysis of collections of male pollock using parasite numbers gave significant results for comparisons based on total numbers of *N. surmenicola* and *A. simplex* (Table 5). STP comparison of collections showed significant differences between all combinations of pairs for both species of parasites. Abundance of both *N. surmenicola* and *A. simplex* increased sharply with host length, with 0.8, 3.6, and 20.2 *N. surmenicola* and 12.6, 23.9, and 43.8 *A. simplex* recovered from small-, medium-, and large-sized male pollock, respectively (Table 5).

For female pollock from Queen Charlotte Sound, significant heterogeneity was demonstrated among collections for prevalence of *N. surmenicola* and *A. simplex* in the musculature, for total *N. surmenicola*, and for *H. aduncum* (Table 6). Subsequent pairwise comparisons revealed no significant differences between collections for total *N. surmenicola* or *H. aduncum*, although for total *N. surmenicola* there was a trend towards increasing prevalence with host length (22/31, 30/31, and 31/31 hosts infected for small-, medium-, and large-sized females, respectively) and for *H. aduncum* there was an opposite trend, with 16/31, 11/31, and 6/31 hosts infected for the three size classes. Pairwise comparisons of prevalence of *N. surmenicola* in the musculature showed small- and medium-sized pollock (4/31 and 5/31 infected, respectively) to differ from large-sized fish (15/31 infected). Similar comparisons of prevalence of *A. simplex* in the musculature showed small female pollock (6/31 infected) to differ from both medium- and large-sized fish (both with 17/31 infected). Analysis of parasite numbers in collections of

TABLE 3. Summary of the results of the Kruskal–Wallis test and STP test for comparison of parasite prevalence and numbers among three length categories of male walleye pollock from Porlier Pass, British Columbia. (*Indicates significant ($P < 0.05$) heterogeneity among collections; **collections not significantly different ($P > 0.05$) when contained within same set of parentheses.)

	Prevalence					Abundance (intensity range)				
	Sm.	Med.	Lg.	H_{adj}	STP summary	Sm.	Med.	Lg.	H_{adj}	STP summary
Nybelinia surmenicola (musculature)	0/28	0/28	0/28	0.000		0.0	0.0	0.0	0.000	
N. surmenicola (total)	0/28	2/28	1/28	2.049		0.0	0.1(1)	0.1(3)	2.001	
Pseudophyllidea	3/28	4/28	4/28	0.207		0.3(1–5)	0.3(1–4)	0.2(1–3)	0.178	
Anisakis simplex (musculature)	3/28	0/28	0/28	6.148*	(Sm,Med,Lg)**	0.2(1–2)	0.0	0.0	6.146*	(Sm,Med,Lg)
A. simplex (total)	14/28	20/28	20/28	3.689		1.0(1–7)	1.0(1–2)	1.9(1–11)	5.702	
Phocanema decipiens	1/28	2/28	1/28	0.519		0.0(1)	0.1(1)	0.0(1)	0.519	
Hysterothylacium aduncum	20/28	17/28	21/28	1.431		2.7(1–23)	2.0(1–14)	1.6(1–12)	1.294	

TABLE 4. Summary of the results of the Kruskal–Wallis test and STP test for comparison of parasite prevalence and numbers among three length categories of female walleye pollock from Porlier Pass, British Columbia. (*Indicates significant ($P < 0.05$) heterogeneity among collections; **collections not significantly different ($P > 0.05$) when contained within same set of parentheses.)

	Prevalence					Abundance (intensity range)				
	Sm.	Med.	Lg.	H_{adj}	STP summary	Sm.	Med.	Lg.	H_{adj}	STP summary
Nybelinia surnenicola (musculature)	0/16	0/16	1/16	2.000		0.0	0.0	0.1(1)	2.000	
N. surmenicola (total)	0/16	0/16	8/16	18.000*	(Sm,Med)(Lg)**	0.0	0.0	1.8(1–13)	18.645*	(Sm,Med)(Lg)
Pseudophyllidea	1/16	2/16	0/16	2.089		0.1(1)	0.1(1)	0.0	2.089	
Anisakis simplex (musculature)	0/16	0/16	2/16	4.087		0.0	0.0	0.1(1–2)	4.085	
A. simplex (total)	5/16	13/16	16/16	19.155*	(Sm)(Med,Lg)	0.6(1–3)	2.0(1–9)	8.3(1–19)	24.765*	(Sm)(Med)(Lg)
Phocanema decipiens	0/16	2/16	2/16	2.136		0.0	0.1(1)	0.2(1–3)	2.136	
Hysterothylacium aduncum	11/16	10/16	10/16	0.178		1.6(1–6)	2.8(1–9)	1.9(1–8)	0.698	

TABLE 5. Summary of the results of the Kruskal–Wallis test and STP test for comparison of parasite prevalence and numbers among three length categories of male walleye pollock from Queen Charlotte Sound, British Columbia. (*Indicates significant ($P < 0.05$) heterogeneity among collections; **collections not significantly different ($P > 0.05$) when contained within same set of parentheses.)

	Prevalence					Abundance (intensity range)				
	Sm.	Med.	Lg.	H_{adj}	STP summary	Sm.	Med.	Lg.	H_{adj}	STP summary
Pleistophora sp.	1/20	6/20	8/20	6.818*	(Sm,Med,Lg)**	—	—	—		
Nybelinia surmenicola (musculature)	0/20	3/20	5/20	5.389		0.0	0.1(1)	2.2(1–38)	5.546	
N. surmenicola (total)	6/20	17/20	20/20	26.312*	(Sm)(Med,Lg)	0.8(1–7)	3.6(1–24)	20.2(1–186)	35.949*	(SM)(Med)(Lg)
Anisakis simplex (musculature)	1/20	5/20	7/20	5.408		0.2(4)	0.9(1–13)	1.6(2–9)	5.790	
A. simplex (total)	19/20	20/20	20/20	2.000		12.6(2–45)	23.9(6–46)	43.8(14–108)	27.712*	(Sm)(Med)(Lg)
Contracaecum-type B	1/20	5/20	3/20	0.876		0.2(1)	0.3(1–2)	0.6(3–5)	0.685	
Phocanema decipiens	1/20	4/20	1/20	3.278		0.0(1)	0.2(1)	0.0(1)	3.278	
Hysterothylacium aduncum	11/20	11/20	12/20	0.133		1.6(3–15)	1.6(2–37)	1.6(9–32)	0.328	

TABLE 6. Summary of the results of the Kruskal–Wallis test and STP test for comparison of parasite prevalence and numbers among three length categories of female walleye pollock from Queen Charlotte Sound, British Columbia. (*Indicates significant ($P < 0.05$) heterogeneity among collections; **collections not significantly different ($P > 0.05$) when contained within same set of parentheses.)

	Prevalence					Abundance (intensity range)				
	Sm.	Med.	Lg.	H_{adj}	STP summary	Sm.	Med.	Lg.	H_{adj}	STP summary
Pleistophora sp.	10/31	8/31	13/31	1.819		—	—	—		
Nybelinia surmenicola (musculature)	4/31	5/31	15/31	12.333*	(Sm,Med)(Lg)**	0.3(1–5)	0.3(1–2)	1.5(1–10)	13.539*	(Sm,Med)(Lg)
N. surmenicola (total)	22/31	30/31	31/31	16.183*	(Sm,Med,Lg)	4.2(1–56)	27.9(2–114)	75.9(1–678)	40.782*	(Sm)(Med,Lg)
Anisakis simplex (musculature)	6/31	17/31	17/31	10.502*	(Sm)(Med,Lg)	0,3(1–3)	2.2(1–20)	4.2(1–47)	12.411*	(Sm)(Med,Lg)
A. simplex (total)	31/31	31/31	31/31	0.000		21.6(4–77)	54.6(8–129)	96.0(26–269)	45.180*	(Sm)(Med)(Lg)
Contracaecum-type B	4/31	9/31	10/31	3.543		0.2(1–3)	0.3(1–2)	0.7(1–7)	3.186	
Phocanema decipiens	6/31	7/31	4/31	0.997		0.3(1–4)	0.2(1)	0.4(1–8)	0.717	
Hysterothylacium aduncum	16/31	11/31	6/31	6.970*	(Sm,Med,Lg)	1.4(1–8)	0.7(1–6)	0.7(1–11)	7.187*	(Sm,Med,Lg)

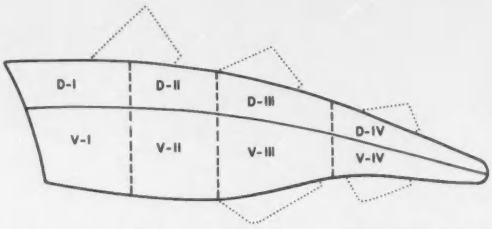

FIG. 2. Diagram of the left body musculature of a walleye pollock showing divisions used for analysis of the distribution of helminths in the flesh. (D = dorsal, V = ventral).

female pollock showed significant heterogeneity among groups for *N. surmenicola* and *A. simplex* occurring in the musculature, for total *N. surmenicola* and *A. simplex*, and for *H. aduncum* (Table 6). Pairwise STP comparisons of collections using numbers of *N. surmenicola* in the musculature showed significant differences between large female pollock and both small- and medium-sized fish, which were similar. Comparisons of total numbers of *N. surmenicola* showed small pollock to differ from both medium- and large-sized fish, which were similar. Abundance of *N. surmenicola* for both total parasites (4.2, 27.9, and 75.9 for small-, medium-, and large-sized fish, respectively) and those occurring in the musculature (0.3, 0.3, and 1.5, respectively) increased with host length (Table 6). Pairwise comparison of collections for numbers of *A. simplex* occurring in the musculature showed small female pollock to differ from both medium- and large-sized fish, which were similar. All comparisons between pairs of collections using total numbers of *A. simplex* were statistically significant (Table 6). Abundance of *A. simplex* increased with host length for counts of nematodes from both the musculature (0.3, 2.2, and 4.2 for small-, medium-, and large-sized fish, respectively) and musculature and body cavity combined (21.6, 54.6, and 96.0, respectively) (Table 6). STP comparison of collections based on numbers of *H. aduncum* did not give significant values for any pair of collections, and examination of abundance for the three collections revealed no trend toward increased or decreased numbers with host size (Table 6).

DISTRIBUTION OF HELMINTHS IN THE MUSCULATURE OF WALLEYE POLLOCK

To examine the distribution of helminths in the musculature of pollock, the left and right body musculature were each divided into four dorsal (epaxial) (I–IV) and four ventral (hypaxial) sections (I–IV) (see Fig. 2). Data used for this portion of the study for *N. surmenicola*, *A. simplex*, and *P. decipiens* were from the more heavily infected Queen Charlotte Sound stock and for pseudophyllidean plerocercoids were from fish from Porlier Pass (Tables 7–10).

Nybelinia surmenicola — Large numbers of plerocercoids of *N. surmenicola* (up to 38 in one host, 37 on the right side and one on the left side) were found only in the mid-ventral (sections II and III) musculature (Table 7). The total percentage of plerocercoids recorded from male pollock for ventral sections II and III was 87.0 and 8.6%, respectively, while that for females was 43.8% for ventral section II and 31.2% for section III. The numbers of *N. surmenicola* in pollock are thus highest in the areas of body musculature surrounding the posterior intestine and gonads, areas of the viscera often heavily infected with this species. Examination of the numbers of helminths recovered from left and right sides of the body showed a high proportion of plerocercoids in male pollock occurring in the right side (93.5 vs. 6.5%). This difference, which was not statistically significant, was due to the infection of the right side of a single host with 37 *N. surmenicola*. Examination of data from the more heavily infected female pollock showed an equal distribution (50.0 vs. 50.0%) of this parasite between left and right sides. Numbers of *N. surmenicola* in pollock therefore do not appear to differ between left and right sides of the body.

Pseudophyllidean plerocercoids — In pollock from Porlier Pass these plerocercoids occurred primarily in the caudal musculature, with intensities ranging from one to five helminths per host. Combined percentages for left and right musculature for male fish showed 26.4% of the plerocercoids in dorsal section III, 10.5% in dorsal section IV, 10.6% in ventral section III, and 47.4% in ventral section IV, or a total of 94.7% of all plerocercoids in the posterior half of the body (Table 8). Females were only rarely infected and two of the three plerocercoids found were located in the posterior half of the body musculature. Although more plerocercoids were observed in the left than the right side of the body musculature, the differences were not statistically significant.

Anisakis simplex — Infection of the musculature of pollock from Queen Charlotte Sound with larval *A. simplex* was primarily in the anterior sections of the ventral musculature surrounding the body cavity (Table 9), with intensity ranging from 1 to 47 helminths per host (Table 6). In male pollock 12.5 and 67.5% of all larvae were found in ventral sections I and II, respectively. Similarly for female fish 37.2% of all larvae were recorded from ventral section I and 50.0% were recorded from ventral section II. No difference was noted in numbers of *A. simplex* between right and left body musculature for male or female pollock.

Phocanema decipiens — Low prevalence and numbers of larval *P. decipiens* were recorded in both dorsal and ventral sections of the musculature of pollock (Table 10). Examination of numbers of parasites revealed no statistical differences among sites of infection.

ANALYSIS OF THE EFFECTS OF STORAGE TIME ON ICE

Results of analysis of parasite prevalence and numbers in four collections of male and female walleye pollock stored in the round on ice at 3°C for periods of 0, 1, 3, and 7 d are presented in Table 11. In all cases no significant heterogeneity among collections was observed, indicating that no detectable movement of parasites either into the musculature from the body cavity or out of the musculature occurred under the conditions of storage tested in this study. Examination of prevalence of infection and abundance for three collections of pollock gutted at capture and stored on ice at 3°C for 0, 3, and 7 d similarly showed that no loss of parasites from the musculature had occurred under these conditions (Table 12).

TABLE 7. Distribution of *Nybelinia surmenicola* plerocercoids in the musculature of walleye pollock from Queen Charlotte Sound, British Columbia.

		Dorsal sections				Ventral sections				All sections combined
		I	II	III	IV	I	II	III	IV	
					Males					
L.S.[a]	No. infected/no. examined	0/60	0/60	0/60	0/60	0/60	1/60	2/60	0/60	
	Intensity range	—	—	—	—	—	1	1	—	
	Total no. parasites	—	—	—	—	—	1	2	—	3
	% of all parasites in both sides	—	—	—	—	—	2.2	4.3	—	6.5
R.S.[a]	No. infected/no. examined	0/60	0/60	0/60	0/60	1/60	3/60	1/60	1/60	
	Intensity range	—	—	—	—	1	1–37	2	1	
	Total no. parasites	—	—	—	—	1	39	2	1	43
	% of all parasites in both sides	—	—	—	—	2.2	84.8	4.3	2.2	93.5
					Females					
L.S.[a]	No. infected/no. examined	1/93	1/93	3/93	1/93	1/93	8/93	3/93	0/93	
	Intensity range	1	1	1	2	1	1–2	1–2	—	
	Total no. parasites	1	1	3	2	1	12	4	—	24
	% of all parasites in both sides	2.1	2.1	6.2	4.2	2.1	25.0	8.3	—	50.0
R.S.[a]	No. infected/no. examined	0/93	1/93	0/93	1/93	1/93	8/93	6/93	0/93	
	Intensity range	—	1	—	1	2	1–2	1–4	—	
	Total no. parasites	—	1	—	1	2	9	11	—	24
	% of all parasites in both sides	—	2.1	—	2.1	4.2	18.8	22.9	—	50.0

[a]L.S. = left side; R.S. = right side.

TABLE 8. Distribution of pseudophyllidean plerocercoids in the musculature of walleye pollock from Porlier Pass, British Columbia.

		Dorsal sections				Ventral sections				All sections combined
		I	II	III	IV	I	II	III	IV	
					Males					
L.S.[a]	No. infected/no. examined	0/86	1/86	2/86	1/86	0/86	0/86	1/86	4/86	
	Intensity range	—	1	1–3	2	—	—	1	1	
	Total no. parasites	—	1	4	2	—	—	1	4	12
	% of all parasites in both sides	—	5.3	21.1	10.5	—	—	5.3	21.1	63.2
R.S.[a]	No. infected/no. examined	0/86	0/86	1/86	0/86	0/86	0/86	1/86	5/86	
	Intensity range	—	—	1	—	—	—	1	1	
	Total no. parasites	—	—	1	—	—	—	1	5	7
	% of all parasites in both sides	—	—	5.3	—	—	—	5.3	26.3	36.8
					Females					
L.S.[a]	No. infected/no. examined	0/49	0/49	1/49	1/49	0/49	0/49	0/49	0/49	
	Intensity range	—	—	1	1	—	—	—	—	
	Total no. parasites	—	—	1	1	—	—	—	—	2
	% of all parasites in both sides	—	—	33.3	33.3	—	—	—	—	66.7
R.S.[a]	No. infected/no. examined	0/49	0/49	0/49	0/49	0/49	1/49	0/49	0/49	
	Intensity range	—	—	—	—	—	1	—	—	
	Total no. parasites	—	—	—	—	—	1	—	—	1
	% of all parasites in both sides	—	—	—	—	—	33.3	—	—	33.3

[a]L.S. = left side; R.S. = right side.

TABLE 9. Distribution of *Anisakis simplex* larvae in the musculature of walleye pollock from Queen Charlotte Sound, British Columbia.

		Dorsal sections				Ventral sections				All sections combined
		I	II	III	IV	I	II	III	IV	
					Males					
L.S.[a]	No. infected/no. examined	1/60	1/60	2/60	1/60	1/60	7/60	0/60	0/60	
	Intensity range	2	—	2	1	2	1–3	—	—	
	Total no. parasites	2	—	2	1	2	14	—	—	21
	% of all parasites in both sides	5.0	—	5.0	2.5	5.0	35.0	—	—	52.5
R.S.[a]	No. infected/no. examined	0/60	0/60	1/60	0/60	3/60	7/60	1/60	0/60	
	Intensity range	—	—	1	—	1	1–4	2	—	
	Total no. parasites	—	—	1	—	3	12	2	—	19
	% of all parasites in both sides	—	—	2.5	—	7.5	32.5	5.0	—	47.5
					Females					
L.S.[a]	No. infected/no. examined	2/93	0/93	1/93	0/93	14/93	20/93	6/93	0/93	
	Intensity range	1	—	1	—	1–9	1–8	1	—	
	Total no. parasites	2	—	1	—	34	56	6	—	99
	% of all parasites in both sides	1.0	—	0.5	—	17.3	28.6	3.1	—	50.5
R.S.[a]	No. infected/no. examined	0/93	1/93	0/93	1/93	11/93	18/93	3/93	0/93	
	Intensity range	—	1	—	1	1–20	1–7	3–8	—	
	Total no. parasites	—	1	—	1	39	42	14	—	97
	% of all parasites in both sides	—	0.5	—	0.5	19.9	21.4	7.1	—	49.5

[a]L.S. = left side; R.S. = right side.

TABLE 10. Distribution of *Phocanema decipiens* larvae in the musculature of walleye pollock from Queen Charlotte Sound, British Columbia.

		Dorsal sections				Ventral sections				All sections combined
		I	II	III	IV	I	II	III	IV	
					Males					
L.S.[a]	No. infected/no. examined	0/60	0/60	0/60	0/60	0/60	2/60	1/60	0/60	
	Intensity range	—	—	—	—	—	1	1	—	
	Total no. parasites	—	—	—	—	—	1	1	—	2
	% of all parasites in both sides	—	—	—	—	—	20.0	20.0	—	40.0
R.S.[a]	No. infected/no. examined	0/60	1/60	0/60	0/60	0/60	1/60	1/60	0/60	
	Intensity range	—	1	—	—	—	1	1	—	
	Total no. parasites	—	1	—	—	—	1	1	—	3
	% of all parasites in both sides	—	20.0	—	—	—	20.0	20.0	—	60.0
					Females					
L.S.[a]	No. infected/no. examined	0/93	0/93	0/93	0/93	0/93	3/93	0/93	1/93	
	Intensity range	—	—	—	—	—	1	—	1	
	Total no. parasites	—	—	—	—	—	3	—	1	4
	% of all parasites in both sides	—	—	—	—	—	25.0	—	8.3	33.3
R.S.[a]	No. infected/no. examined	0/93	1/93	5/93	1/93	0/93	0/93	1/93	0/93	
	Intensity range	—	1	1	1	—	—	1	—	
	Total no. parasites	—	1	5	1	—	—	1	—	8
	% of all parasites in both sides	—	8.3	41.7	8.3	—	—	8.3	—	66.7

[a]L.S. = left side; R.S. = right side.

TABLE 11. Results of the Kruskal–Wallis test for analysis of the effect of storage time on ice on the prevalence of infection and numbers of parasites occurring in the musculature of walleye pollock from Porlier Pass, British Columbia, stored as round fish.

Days on ice	Prevalence					Abundance (intensity range)					
	0	1	3	7	H_{adj} [a]	0	1	3	7	H_{adj}*
Males										
Nybelinia surmenicola	0/19	0/16	0/18	0/18	—	—	—	—	—	—
Pseudophyllidea	3/19	2/16	3/18	1/18	1.233	0.3(1–3)	0.1(1)	0.3(1–4)	0.1(1)	1.326
Anisakis simplex	1/19	0/16	0/18	2/18	3.608	0.1(1)	—	—	0.2(1–2)	3.647
Phocanema decipiens	0/19	2/16	2/18	0/18	4.578	—	0.1(1)	0.1(1)	—	4.578
Hysterothylacium aduncum	0/19	0/16	0/18	0/18	—	—	—	—	—	—
Females										
Nybelinia surmenicola	0/6	0/7	0/6	0/6	—	—	—	—	—	—
Pseudophyllidea	0/6	1/7	0/6	2/6	1.297	—	0.1(1)	—	0.3(1)	1.297
Anisakis simplex	0/6	0/7	0/6	0/6	—	—	—	—	—	—
Phocanema decipiens	0/6	2/7	0/6	1/6	3.437	—	0.3(1)	—	0.2(1)	3.437
Hysterothylacium aduncum	0/6	0/7	0/6	0/6	—	—	—	—	—	—

[a] None of the values indicate significant ($P < 0.05$) heterogeneity among collections.

Discussion

The results show that the prevalence and abundance of parasites infecting the musculature and body cavity of pollock are, in some cases, a function of host length and that differences between male and female pollock of the same length may occur. Differences in prevalence and abundance of species such as *N. surmenicola* and *A. simplex* between male and female pollock of the same length have not previously been noted. These differences may be attributed to sex-related differences in host growth rates. Female pollock are known to grow more rapidly than males and are thus from 3 to 8 cm longer than male fish in the Queen Charlotte Sound stock at age 3 or greater (Thompson 1981). Because male pollock are older than females at a given length, they can be expected to have greater numbers of long-lived species of parasites such as *A. simplex* and *N. surmenicola* that are accumulated with increasing host age.

Quantitative and qualitative changes in the parasite fauna of marine fishes with host age have been extensively documented and have been related to such factors as changes in the composition and quantity of host diet with age, with development of age-acquired immunity to certain species, the effects of host migrations, and the accumulation with age of long-lived species of parasites (see, for example, Kahl 1939; Polyansky and Shulman 1956; Polyansky 1958; Kagei 1969; Reimer and Jessen 1972). The results of this study have similarly shown that host age, as reflected by length, is an important factor in determining the prevalence and abundance of parasites occurring in the musculature and body cavity of walleye pollock. Of the five species of parasites infecting the musculature and body cavity of pollock from Porlier Pass or Queen Charlotte Sound, at least three (*Pleistophora* sp., *N. surmenicola*, and *A. simplex*) occur more frequently or with greater numbers in larger fish. Very strong accumulation with increasing host length was evident for total numbers of *N. surmenicola* and *A. simplex*, particularly for male and female pollock belonging to the more heavily infected stock from Queen Charlotte Sound. Prevalence and numbers for *A. simplex* and *N. surmenicola* occurring only in the musculature showed similar though often nonsignificant trends toward increasing values with host length.

No previous studies have investigated in detail the role of host length in determining the prevalence or abundance of parasites infecting walleye pollock. Grabda (1977), who identified 11 species of parasites from examination of pollock imported to Poland from the Soviet Union, noted that the percentage of uninfected fish decreased with increased host length but did not discuss individual species of parasites separately. Similar observations, also of a general nature, have been made by Mamaev and Baeva (1963). Sasaki (1973) noted that prevalence of infection of Japanese walleye pollock by *N. surmenicola*, *Pyramicocephalus phocarum*, and anisakid nematodes was higher in fish over 300 mm in length than in those of smaller size, and that pollock of less than 400 mm were uninfected by microsporidan cysts. Hughes and Alton (1974) similarly reported increased prevalence of infection of the musculature of Alaska walleye pollock by unidentified nematodes and cysts of undetermined origin. Numerous studies have reported increased infection with host length for other species of marine fishes infected with long-

TABLE 12. Prevalence and abundance of parasites of the musculature of walleye pollock from Porlier Pass, British Columbia, gutted at capture and stored on ice.

	Prevalence			Abundance (intensity range)		
Days on ice	0	3	7	0	3	7
Pseudophyllidea	3/25	3/25	2/25	0.2(1−3)	0.2(1−2)	0.2(2)
Anisakis simplex	1/25	2/25	1/25	0.0(1)	0.1(1−2)	0.1(2)
Phocanema decipiens	0/25	2/25	2/25	—	0.1(1)	0.1(1−2)

lived larval helminths such as *Anisakis* (see, for example, Bishop and Margolis 1955; Muravev 1970; Davey 1972), and it appears, in general, that most larval or cyst-producing parasites infecting marine fishes may be accumulated with increased age given that the host is exposed to infective stages throughout its life history.

Numerous studies and observations have been made on the distribution of larval helminths in the flesh of marine fishes. Similar observations noting high intensity of infection of the ventral musculature surrounding the abdominal cavity (belly flaps) by larval *Anisakis* have been made, for example, by Smith and Wootten (1975) for Atlantic herring (*Clupea harengus harengus*) and whiting (*Gadus merlangus*), by Young (1972) and Platt (1975) for Atlantic cod (*Gadus morhua*), by Novotny and Uzmann (1960) for chum salmon (*Oncorhynchus keta*), and by Grabda (1977) for walleye pollock. Previous studies recording the more frequent occurrence of *N. surmenicola* plerocercoids in the ventral musculature of pollock are those of Oshmarin et al. (1961), Mamaev and Baeva (1963), Sasaki (1973), and Grabda (1977). The distribution of *P. decipiens* in the muscle of cod has been investigated by Young (1972), who found that in fish less than 50 cm in length nematode larvae occurred in approximately equal numbers in the belly flaps and in the remainder of the body musculature. In larger cod, infection by *P. decipiens* was heavier in the former site. Templeman et al. (1957), in a study on the distribution of larval nematodes (*Phocanema* and *Anisakis*) in the fillets of cod from Canadian Atlantic waters, noted that infection occurred primarily in those areas of the fillet nearest the body cavity.

The evaluation of the role of handling methods in affecting the prevalence and abundance of aesthetically objectionable or potentially pathogenic species of parasites occurring in the musculature of commercially important marine fishes has received considerable study, with particular attention having been given the effect of storage temperature on infection of the musculature by *Anisakis* larvae (see, for example, Khalil 1969; Davey 1972; Smith and Wootten 1975). Similar though less-detailed studies have been conducted on *N. surmenicola* and *Anisakis* sp. in walleye pollock. Oshmarin et al. (1961) concluded that pollock kept at low temperatures (−2 to 8°C) for storage times of up to 36 h were suitable for commercial processing, but the storage of fish at higher temperatures (12−48°C) resulted in the migration of plerocercoids of *N. surmenicola* from the body cavity and viscera into the musculature. Gusev et al. (1959), Mamaev and Baeva (1963), and Mamaev et al. (1965) have similarly remarked on the postmortem migration of *N. surmenicola* plerocercoids under storage conditions. Kazykhanov and Slipchenko (1970) have noted that at temperatures prevailing during the Soviet pollock fishery, plerocercoids of *N. surmenicola* do not undertake any migration within the host for at least 2 d after capture. Suzuki and Oishi (1974) compared parasite intensities for eight randomly selected pollock examined on capture with those for nine fish stored at room temperature (18.2−21.0°C) for 24 h and concluded that significant migration from the viscera into the musculature had occurred for *Anisakis* sp., *N. surmenicola*, and *Contracaecum* sp. Although an in-depth, carefully controlled study has not been accomplished, the above observations indicate that at relatively high temperatures of storage parasites encapsulated in the body cavity of pollock may leave their capsules and migrate into the body musculature. Similar but more appropriately designed experiments conducted on *Anisakis* sp. in Atlantic herring by Smith and Wootten (1975) indicate that a significant increase in the numbers of larval nematodes in the flesh of herring may occur at temperatures as low as 3°C. Because migration of nematodes under these experimental conditions could not be due to temperature stimulation, these authors postulated that they may be triggered by physicochemical changes in the host viscera. No comparable migration of larval *A. simplex* or *N. surmenicola* was noted in walleye pollock stored for up to 7 d under conditions similar to those used by these authors. Because postmortem migration of encapsulated helminths is clearly more likely to take place at high temperatures, the results obtained in the present study may in part be attributable to the low storage temperature (3°C) used and perhaps also, in the case of *N. surmenicola*, to the low abundance of this species in the stock of pollock used in this experiment, which would tend to make detection of any migration more difficult.

Comparison of the abundance of parasites infecting the musculature and body cavity of pollock from British Columbian waters with that previously reported from other areas of the North Pacific Ocean is difficult because of differences in host lengths, sex composition, and size of collections. However, it appears that parasites are less abundant in pollock from southern British Columbia (i.e. Strait of Georgia) than in any stock previously examined. The abundance of parasites in pollock from northern British Columbia (i.e. Queen Charlotte Sound) appears to be similar to that reported for some other areas of the North Pacific Ocean (see Zhukov 1960; Strelkov 1960; Oshmarin et al. 1961; Skrjabina 1963; Mamaev and Baeva 1963; Sasaki 1973; Suzuki and Oishi 1974), but not as high as for the most heavily infected northwest Pacific areas.

Under current methods employed in the handling and processing of walleye pollock in British Columbia, parasites are unlikely to present a serious problem to commercial exploitation of fish from the Porlier Pass area. Pollock from other areas, such as Queen Charlotte Sound, may be heavily infected by *N. surmenicola*, *A. simplex*, or *Pleistophora* sp. However, practices applied in the production of fillets by the

industry result in removal and discarding of areas of musculature most often infected and the destruction by freezing of any remaining parasites of public health significance. In addition, a sustained high rate of exploitation of British Columbia pollock stocks with accompanying removal of the older, more heavily infected fish may be expected to reduce the percentage of highly infected pollock captured.

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An Allometric Model for Pesticide Bioaccumulation

SARA GRIESBACH AND ROBERT HENRY PETERS

Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1

AND SAMI YOUAKIM

Marine Sciences Centre, McGill University, 3620 University Street, Montreal, Que. H3A 2B2

GRIESBACH, S., R. H. PETERS, AND S. YOUAKIM. 1982. An allometric model for pesticide bioaccumulation. Can. J. Fish. Aquat. Sci. 39: 727 – 735.

A combination of the frequency distribution of body sizes and appropriate allometric relationships may permit a more operational approach to pesticide bioaccumulation than the more traditional trophic level concept. To demonstrate this potential, we describe patterns of bioaccumulation as functions of time and body size in a computer ecosystem in which no differences in trophic level exist. The qualitative similarity between these patterns and those reported in the literature from laboratory and field experiments suggests that empirical relations describing contaminant fluxes as functions of body weight could form a powerful base for the prediction of contaminant body burden in natural systems. We believe this approach could prove useful for any persistent contaminant with high biological affinity.

Key words: modeling, bioaccumulation, ecological magnification, allometry, body size

GRIESBACH, S., R. H. PETERS, AND S. YOUAKIM. 1982. An allometric model for pesticide bioaccumulation. Can. J. Fish. Aquat. Sci. 39: 727 – 735.

Une approche de la bioaccumulation de pesticides plus opérationnelle que le concept traditionnel du niveau trophique pourrait résulter d'une combinaison de la distribution des fréquences de taille corporelle avec des relations allométriques appropriées. Nous démontrons cette possibilité en décrivant des schémas de bioaccumulation comme fonctions du temps et de la taille corporelle dans un écosystème où n'existent pas de différences de niveaux trophiques. La similarité qualitative observée entre ces schémas et ceux publiés à la suite d'expériences en laboratoire et sur le terrain donnent à penser que des relations empiriques décrivant les flux de contaminants comme fonctions du poids corporel pourraient servir de base solide à la prédiction de charges corporelles de contaminants dans les systèmes naturels. À notre avis, cette approche serait utile pour tout contaminant persistant de haute affinité biologique.

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BIOACCUMULATION of organochlorines and other compounds is usually considered an effect of contaminant transfer along food chains. Unfortunately, this conceptual approach can have only limited predictive success because the basic terms — food chains, food webs, and trophic levels — are difficult, if not impossible, to define operationally (Eberhardt 1969; Isaacs 1973; May 1979; Peters 1977; Rigler 1975). In any case, the exact trophic position of any animal becomes increasingly uncertain among higher predators (Lindemann 1942) where ecological magnification is most pronounced, or in aquatic systems where rigid food choice is the exception (Isaacs 1973) and contaminant accumulation, perhaps, most studied. Other variables, such as metabolic rate (Boddington et al. 1979; Neely 1979; Norstrom et al. 1976), lipid content (Hamelink et al. 1971), and body size (Thomann 1978, 1981; Woodwell et al. 1967), also influence ecological magnification. Because such characteristics are more measurable, they are also more amenable to the construction of quantitative theory.

Of these alternatives, the most attractive is body size, simply because it is most easily determined. Previous models have employed body size, but these models usually apply only to single species (Fagerström et al. 1974; Norstrom et al. 1976) or invoke food chains as well as body size (Thomann 1978, 1981). We feel that patterns of bioaccumulation in animal communities may be predictable from empirical relations describing contaminant uptake and release as functions of body size. Unfortunately, this hypothesis cannot be tested until the appropriate allometric relations are developed. In the hope that a demonstration of the potential of such an approach to bioaccumulation might hasten its development, this paper compares previously observed patterns of bioaccumulation with those produced in a generalized ecosystem described by allometric equations. If model and observations are qualitatively similar, then body size could be a powerful enough

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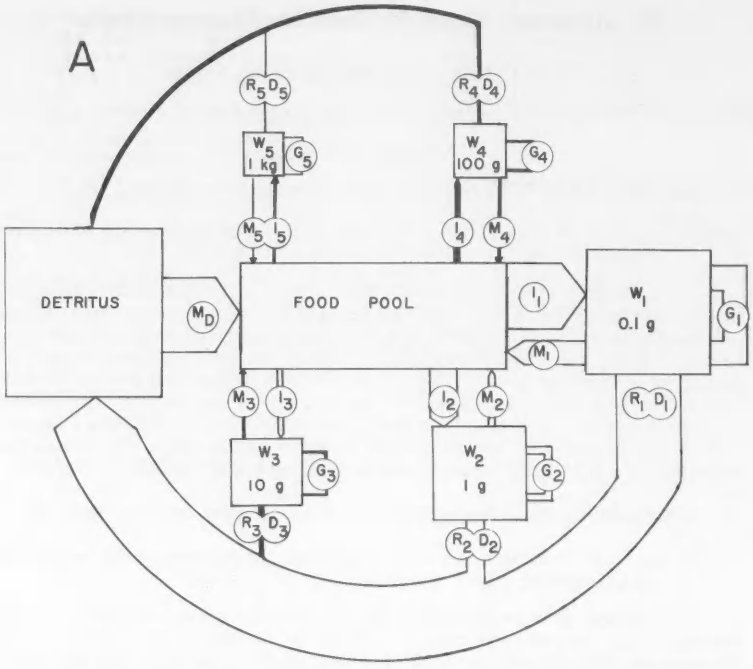

FIG. 1A. Mass flow at steady state in a model ecosystem containing 100 kg of material distributed among a detrital compartment and five living compartments of total biomass B_i containing organisms of individual body mass W_i. Fluxes (in g/d) among these compartments are defined by equations 1–5 which describe ingestion (I_i), production (G_i), respiration (R_i), and defecation (D_i) as functions of individual body size and compartment size. Mortality losses (M_i) are determined by community food demands and compartment size. The area of the six compartments has been drawn proportional to their size at steady state, and the widths of connecting arrows is proportional to daily flux. The food pool has been drawn disproportionately large; its true size would be slightly less than that of W_5.

determinant of ecological magnification to warrant intensive study.

An Allometric Model of Biomass Flux

The computer "ecosystem" (Fig. 1A) in which bioaccumulation occurred is a bioenergetics model (Peters 1978) containing a "detrital" pool (D, in g) and five size classes of "poikilothermic organisms", described by individual body mass (W_i, in g) and total biomass (B_i, in g). The rates of ingestion (I_i, in g/d), production or growth (G_i, in g/d), and respiration (R_i, in g/d) of each size class are derived from empirical allometric equations such that

$$(1) \quad I_i = B_i \cdot 0.033 W_i^{-0.25},$$

$$(2) \quad G_i = B_i \cdot 0.01 W_i^{-0.25},$$

$$(3) \quad R_i = B_i \cdot 0.01 W_i^{-0.25}.$$

The relations for ingestion and production are modified from Farlow (1976) and that for respiration from Hemmingsen (1960). In each equation, the original units (kcal/d) were converted to fresh mass (g/d) by assuming 1.6 kcal (6.7 kJ) equals 1 g. The exponents were standardized at -0.25 to avoid size-related differences induced by slight variations in the exponent which may only represent random variations within the original data sets (Hemmingsen 1960). Defecation (D_i, in g/d) was determined by difference

$$(4) \quad D_i = I_i - (R_i + G_i).$$

The components in this ecosystem were then linked by a mortality function which describes daily losses (M_i, in g/d) from each compartment including detritus as a function of relative compartment size and total predation level (ΣI_i):

$$(5) \quad M_i = [B_i^f / (D^f + \Sigma B_i^f)]\, \Sigma I_i.$$

Losses from the detrital compartment were determined by replacing B_i in the numerator with D. This equation assumes that all losses through mortality are consumed by the remaining members of the community. In other words, total mortality (ΣM_i) is set by and equivalent to community food demands (ΣI_i). Daily respiration and defecation losses ($\Sigma R_i + \Sigma D_i$) were replaced by equivalent additions to the detrital pool so that total ecosystem size remained constant. Initially all size classes were assigned equal biomasses; at "daily" intervals, gains and losses were calculated from equations 1 to 5 until an effectively stable distribution in biomass

TABLE 1. Equilibrium values for coefficients of flux in the bioenergetic and contaminant models. Because these depend only on biomass (B_i) and individual size (W_i), they are effectively constants at equilibrium.

Coefficient	Compartment					
	D	1	2	3	4	5
W_i (g)	—	0.1	1	10	100	1000
$W_i^{-0.25}$	—	1.78	1	0.56	0.32	0.18
B_i(kg)	45.9	25.1	14.2	7.9	4.5	2.5
$B_iW_i^{-0.25}$	—	44.7	14.2	4.42	1.44	0.45
R_i (g/d)	—	450	140	45	14	4.5
G_i (g/d)	—	450	140	45	14	4.5
D_i (g/d)	—	600	180	60	18	6.0
I_i (g/d)	—	1500	460	150	46	15
I_i/I_i	—	0.69	0.21	0.069	0.021	0.0069
M_i (g/d)	1500	450	140	45	15	4.5
M_i/I_i	0.69	0.21	0.067	0.021	0.0069	0.0021
$M_i/B_i^{(d-1)}$	0.033	0.018	0.010	0.0057	0.0033	0.0018
B_i^f	2100	620	200	62	20	6.2

was attained. Previous experience with this model (Peters 1978) has shown that each size class persists only if the higher productivity of smaller organisms is offset by increased mortality. This is achieved by selecting values of f in equation 5 which are greater than 1. In this paper, f was assigned the value 2 because the steady-state distribution of biomass, produced by this choice, approximates the size frequency distribution of, at least, one natural system, the freshwater plankton (Peters 1978). Because equations 1 to 5 are functions of class biomass and individual body size, the values of I_i, D_i, G_i, R_i, and M_i are constants at steady state. Their equilibrium solutions are given in Table 1 which shows that both class sizes and fluxes decline with individual size. This is shown graphically in Fig. 1A.

The model's most distinctive characteristic lies in its trophic relations. Essentially, daily mortality losses are summed in a common food pool and then distributed to the five organismic classes according to their food demands. The food pool in Fig. 1A is drawn disproportionately large: its size is equivalent to daily community mortality (ΣM_i) or ingestion (ΣI_i), 2.1 kg. All organisms in this ecosystem eat the same type of food: this implies that no food chain exists and that all organisms are at the same trophic level. This is not a denial of the existence of differences in food preference among individual organisms and species. It is an assertion that, given the variety of potential foraging strategies — planktivory, detritivory, piscivory, coprophagy, etc. — open to members of a multispecific size class, trophic interaction may be approximated as well by an unstructured food web as by a more complex model. The absence of trophic structure is an abstraction to achieve tractability.

Modifications to Treat DDT Flux and Accumulation

This model can be modified to include realistic assumptions relating contaminant flux to body size. However, if differences in trophic level are the essential feature of ecosystem function which leads to bioaccumulation, this modified model should not produce realistic patterns of body burden. In fact, because all organisms in the model eat the same food, one would suspect that eventually similar levels of contamination would be observed in all size classes. However, if, as we suspect, allometric differences play a major role in pesticide bioaccumulation, the model should be capable of generating realistic patterns of contamination in the five size classes. Like tests of all theories, this test is asymmetrical: a successful imitation of nature would not imply that ecological magnification is necessarily the result of body size effects, only that such effects may provide a possible mechanism. However, if an allometric model cannot simulate observation, this would suggest that body size relations are not important in bioaccumulation.

To treat any contaminant, we must modify the model to permit the calculation of daily uptake and loss of that material by each compartment. Because the only characteristics of the organisms in these classes are total biomass and individual weight, the equations describing contaminant fluxes must be expressed in those terms. Ideally the relations would be empirically defined, but given the paucity and contradictions of the current data base, relative to that supporting the bioenergetic relations, we were forced to use reasonable assumptions instead.

Conceptually we chose to model a DDT-like material, for we assumed that the contaminant would be readily absorbed by the biota (Addison 1976; Södergren 1968) and that it persists for long periods (Woodwell et al. 1967). Specifically, the contaminant model (Fig. 1B) assumes that a pulse of DDT is delivered to a dissolved or free pool (P_{free}) in the bioenergetics model after a steady state with respect to biomass had been achieved (Fig. 1A). DDT was then taken up by direct absorption (Ap_i) and redistributed by ingestion (Ip_i), assimilation (set as a constant fraction of ingestion (AE)) defecation (Dp_i), and mortality losses (Mp_i). A mass balance equation for the amount of pesticide ($P_{i,t+1}$) in any compartment i at time $t+1$ can be written as

$$(6) \quad P_{i,t+1} = P_{i,t} + Ap_i + AE \cdot Ip_i - Mp_i$$

where $P_{i,t}$ is the amount of pesticide in that compartment at time t.

Direct uptake by size class (Ap_i in μg/d) is proportional to metabolic rate (Boddington et al. 1979; Neely 1979),

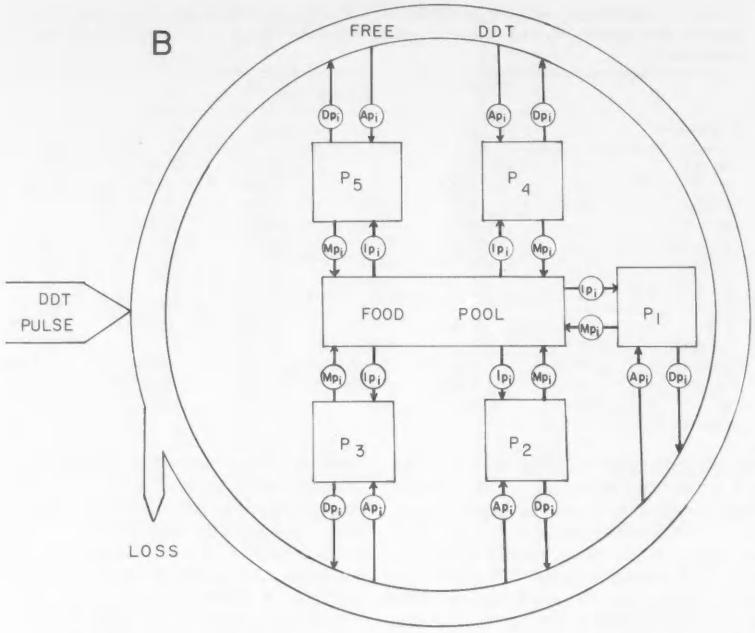

FIG. 1B. DDT flux in the model. P_i(μg) is the amount of DDT in each compartment and the lower case p indicates that pesticide flow (μg/d) is being considered in relation to the pathways of Fig. 1A plus direct uptake (Ap_i) of free DDT. The amount of pesticide in each compartment and the magnitude of each flux changes with time after the addition of a pulse of DDT at zero time.

and 75% of the free DDT was absorbed per day:

$$(7) \quad Ap_i = 0.75\ P_{free} \cdot W_i^{-0.25} \cdot B_i / \sum(B_i \cdot W_i^{-0.25}).$$

Because the equilibrium value of $W_i^{-0.25} \cdot B_i$ declines with size (Table 1), this mimics the nearly complete association of free organochlorines with living organisms in nature and the more rapid uptake of such materials by smaller organisms (Brown 1978; Johnson et al. 1971; Reinert 1972).

DDT was assumed to mix completely in each compartment; thus mortality losses from that compartment involved a proportionate loss of pesticide (Mp_i, in μg/d) calculated as

$$(8) \quad Mp_i = P_i \cdot M_i / B_i$$

in compartment i where P_i is the amount of pesticide. Because the mortality term, M_i, is described by equation (5) as a declining function of individual size and biomass (Table 1), this equation increases the rate of turnover of pesticide among small organisms. In the absence of compensatory pesticide uptake, this leads to more rapid cleansing of contaminated compartments containing smaller individuals. These daily losses were again summed in a common food pool (ΣMp_i) and then distributed to each class in proportion to their food demands. This food pool is a bookkeeper's abstraction with no empirical counterpart. It represents the total amount of pesticide lost through mortality on a given day and therefore the amount which is ingested. The food pool should not be confused with potentially available food, for the contents of all compartments are potentially available.

Pesticide ingestion rate (Ip_i in μg/d) of each compartment is therefore calculated as

$$(9) \quad Ip_i = I_i \cdot \sum Mp_i / \sum I_i.$$

As ingestion rate (I_i) of each class depends on specific ingestion rate and class biomass (equation 1), this calculation implies that a disproportionate amount of the total ingested pesticide is consumed by smaller organisms (Table 1). Equation (9) also assumes that pesticide is homogeneously mixed in the food and so that the pesticide concentration of the ingesta ($\Sigma Mp_i / \Sigma I_i$) is a temporally varying constant for all compartments. In other words, the contaminant concentration of the food of all size classes is a function of contaminant levels in the entire ecosystem, rather than a reflection of specific food choice by each predator. This is a specific effect of the model's lack of a trophic hierarchy.

Assimilation efficiency of DDT was set at 90%, an empirical value for fats (Davison et al. 1978) in which intrabiotic DDT is dissolved (Hamelink et al. 1971). Daily pesticide defecation (Dp_i, in μg/d) is therefore calculated as

$$(10) \quad Dp_i = 0.1 \cdot Ip_i.$$

Because Fagerström (1977) has shown that closed models dominated by allometric relations lead to a uniform distribution of trace compounds like DDT, not bioaccumulation, the present model was opened by allowing a daily loss (μg/d) of

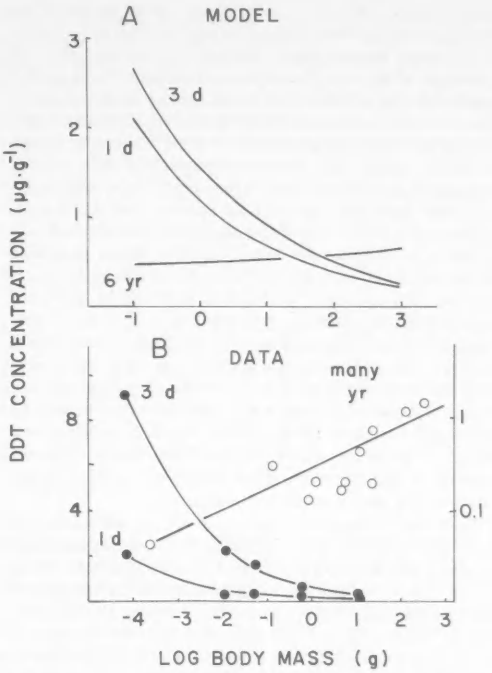

FIG. 2. Comparison of initial and final trends in DDT concentration (A) in the model as a function of weight after the addition of a pulse of 100 mg of DDT with (B) similar data from the literature (Johnson et al. 1971; Woodwell et al. 1967). Individual body sizes were estimated from various sources for Fig. 2B. The right axis in Fig. 2B applies to results after many years. Both model and data show that small organisms initially have the highest burdens and that large organisms have the highest burdens after many years. Differences in the absolute concentrations in Fig. 2A and B are incidental (see text).

50% of defecated DDT from the system.

(11) $\text{Loss} = 0.5 \cdot Dp_i$.

The mass balance for the free DDT pool at any time $t + 1$ ($P_{\text{free}\cdot t+1}$) is therefore

(12) $P_{\text{free}\cdot t+1} = P_{\text{free}\cdot t} + 0.5 \cdot \sum Dp_i - \sum Ap_i$

where $P_{\text{free}\cdot t}$ is the amount of free pesticide at time t. Fecal sedimentation is thought to be a significant sink in pelagic systems (Ferrante and Parker 1977; Peters and Rigler 1973; Schrader 1971), and the assumed loss rate in equation 11 resulted in a half-life for DDT of 3.1 yr. This is in the range of published values for aquatic systems (Brown 1978; Nash and Woolson 1967), but this correspondence is largely fortuitous. Empirically determined half-lives are based on water samples and largely reflect the retention of contaminant by the plankton. The present model lacks a plankton compartment and the half-life reflects retention in big animals which are largely ignored in empirical estimates of half-life. Unsedimented fecal DDT was assumed to pass to the free pool where it was subject to reabsorption. This recycling of fecal DDT serves as an alternative to an excretion term. There is no explicit excretion term in the basic model because the literature provided little consistent evidence as to its relationship with body size (Harding and Vass 1979; Khan 1977; Norstrom et al. 1976; Thomann 1978). The release of soluble DDT in the feces could be considered functionally equivalent to excretion if clearance were proportional to ingestion rate (and hence to $W^{-0.25}$) and to the pesticide concentration of the food. This would be an acceptable approximation in treating the flow of phosphorus (Peters 1975) or carbon (Lampert 1975), but need not apply to pesticides. Many of our assumptions can be relaxed without affecting our argument (see below) and would undoubtedly differ if empirical estimates were available. We believe that this model can apply, with modification, to any persistent contaminant with a high biological affinity.

Comparisons Between Model and Observations

Figure 2 compares the initial and final patterns of bioaccumulation achieved under these assumptions with relevant data from the literature. Immediately after the DDT pulse, rapid rates of absorption led to high levels of contaminant in the smallest organisms. With time, redistribution of DDT by assimilation, growth, and mortality caused the maximum concentration to move to successively larger organisms until the biggest animals had the highest body burden (Fig. 2A). Qualitatively similar trends (Fig. 2B) are observed in real systems (Johnson et al. 1971; Woodwell et al. 1967). Several differences exist between the model and the data with which it is compared. This is scarcely surprising because we made no attempt to simulate the data by adjusting constants in the model. For example, after 3 d the body burden of the smallest organisms in the model is less than that observed in the smallest organisms used in experiments. This reflects differences in absolute size, for the levels in organisms weighing 0.1 g are more similar to each other. However, the absolute levels of contaminant in the model are a direct function of the DDT pulse: if one wished, one could easily raise or lower the predicted concentrations by changing pulse size. Similarly, the increase in body burden between 1 and 3 d is less in the experiment than in the model. The initial accumulation of DDT is largely a function of the assumed daily direct absorbtion of DDT. Because the model assumed that 75% was absorbed in the 1st day, subsequent absorbtion must be relatively small. If a lower figure for absorbtion had been used, the model would generate curves which were quantitatively more similar. Finally, the slope relating concentration to body size after many years is steeper than that generated after 6 yr by the model. This is a more distressing difference because the model seems incapable of producing so steep a slope without the introduction of an excretion term or greatly increasing sedimentation losses (section on sensitivity analysis, below). On the other hand, the data after many years were not obtained in an experimental system, but from a marsh on Long Island where the assumption of a single pulse of DDT is undoubtedly inapplicable. The model would be able to generate steeper curves if the single pulse were replaced with a loading function which describes DDT input as a declining function of time. Similarities between model and observations could therefore be improved, but it is not our purpose to

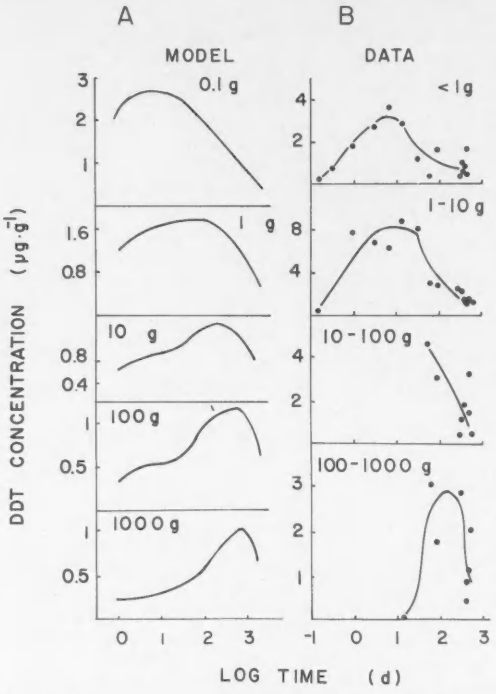

FIG. 3. Temporal changes in pesticide level in organisms of different size (A) as predicted by the model and (B) as observed experimentally in a freshwater marsh. As in Fig. 2, the model generates qualitatively similar trends, and differences in absolute levels are not important. The most significant difference between prediction and observation is the relatively low burden of the smallest size class in the marsh (see text). In Fig. 3B, the upper panels represent the average total body concentration observed in invertebrates (uppermost panel) and small fish (2nd panel) at each sample data, and the lower panels represent average residues found in the livers of poikilothermic vertebrates after the addition of a pulse of radioactive DDT. The size range of individuals in each class (Fig. 3B) is written near the top of each panel. The mass of invertebrates was not given (Meeks 1968) but was usually less than 1 g.

simulate previous results by ad hoc adjustments. We find qualitative comparisons with the unadjusted model already indicate that allometric relations might play an important role in ecological magnification.

The temporal pattern within each of the model's size classes (Fig. 3A) is qualitatively similar to that observed (Fig. 3B) when radioactive DDT was added to a freshwater marsh (Meeks 1968). The time at which peak contamination occurred was increased in larger size classes, but the absolute concentration of this maximum was less for larger animals. Again there are differences between model and data. In larger size classes, the absolute levels in the model are only one quarter those in the marsh. This again is of little significance and could be removed by raising the DDT pulse from 100 to 400 mg or by reducing ecosystem size from 100 to 25 kg. Also, intensive sampling of the marsh over the 1st day of study allowed a relatively complete picture of the initial increases in contaminant level in the two smallest size classes. These do not appear in the model because the first point was generated after 1 d. Shorter time increments in the model would have produced a more similar initial trend but would have markedly and unnecessarily increased computing costs. A more significant difference occurs in the smallest size classes. In the model, rapid absorbtion causes this class to reach the highest absolute burdens. In the marsh, the second smallest class developed the highest burden, and the macroinvertebrates which form the smallest size class showed only moderate levels of contamination. In nature, direct absorbtion by macroinvertebrates may play a smaller role than the model suggests because much of the free contaminant is instead absorbed by the plankton. However, this effect would only influence the absolute level of pesticide. Even if absorbtion is greatly reduced, the model's smallest size class will always have the highest maximum body burden. The relatively low values of the smallest class in Fig. 3B cannot be simulated by minor adjustment of the model and therefore reflect a real difference between model and nature. This must be explained in terms of differences in habitat, physiology, or food preferences which are not related to body size.

Some shortcomings must be expected from the model, for its results were obtained in isolation from the measurements to which they have been compared. Quantitative tests of the model require at least the measurement of DDT uptake and loss as a function of body size and the size frequency distribution of biomass in the ecosystem in which the test will be performed. Until this can be done, the qualitative similarities between the model's response and actual data are sufficiently strong to suggest that further study may prove profitable. If position in the food chain were the main determinant of pesticide accumulation, it would seem unlikely that organisms eating the same food should have differences in body burden. In contrast, this model suggests that size alone can influence the level of contamination even if no differences in food exist.

Sensitivity Analyses

We realize that correspondence between prediction and observation can never prove that theory is correct, and computer models can easily be right for the wrong reason. However, in this case, we believe the similarity is not fortuitous, but reflects the overriding importance of allometric relations in animal physiology and the relatively small effect of trophic structure on material flow in some ecosystems. The model's results do not seem to depend on the necessary assumptions regarding DDT uptake and loss from the system. Different values for direct absorption of DDT from the water (10−100% d^{-1}) had almost no effect on trends in toxicant concentrations (Table 2). Higher sedimentation losses led more rapidly to more pronounced increases in body burden with size, but to lower absolute concentrations; lower sedimentation losses led to less pronounced size effects, higher absolute levels, and to slower movement of DDT through the system. Changes in assimilation efficiency had similar effects: a decrease in assimilation efficiency increased the amount of defecated DDT and so increased sedimentation loss. Thus the model suggests that the assimilation efficiency and the fate of defecated DDT are important terms which

TABLE 2. Sensitivity analysis of the effects of assumed values for the proportion (*AB*) of free DDT absorbed daily by organisms in the model, the proportion (*AE*) of total DDT ingested that is absorbed into an organism's body, and the proportion (*L*) of defecated DDT that is lost from the system. Listed values are the body burdens (μg/g) in each size class 2 yr after a pulse of DDT.

	Parameter			Size class				
	AB	*AE*	*L*	0.1	1.0	10	100	1000
1.	1.00	0.90	0.50	1.14	1.18	1.24	1.24	1.24
2.	0.10	0.90	0.50	1.14	1.18	1.23	1.23	1.07
3.	0.75	1.00	0.50	1.88	1.88	1.88	1.77	1.47
4.	0.75	0.95	0.50	1.46	1.49	1.52	1.47	1.25
5.[a]	0.75	0.90	0.50	1.14	1.18	1.23	1.23	1.07
6.	0.75	0.75	0.50	0.55	0.59	0.68	0.75	0.70
7.	0.75	0.50	0.50	0.16	0.20	0.27	0.36	0.38
8.	0.75	0.10	0.50	0.03	0.04	0.08	0.15	0.19
9.	0.75	0.90	0.90	0.78	0.82	0.90	0.94	0.85
10.	0.75	0.90	0.75	0.90	0.94	1.01	1.04	0.92
11.	0.75	0.90	0.25	1.46	1.49	1.52	1.47	1.25
12.	0.75	0.90	0.10	1.70	1.71	1.72	1.64	1.38

[a]Basic model.

should be determined empirically, because both influence the partitioning of DDT between the biota and its environment. This observation implies that the role of abiotic processes will modify the effects of physiological processing (Thomann 1981) and explains our restriction of the model to materials with high biological affinities. For such materials, sensitivity analysis suggests that empirically based models similar to that discussed here may well result in differences in the timing of peaks and in the relative burdens of different size classes.

The model was further modified by directing that portion of defecated DDT which was not sedimented to enter the detrital pool from which it was assimilated by the organism with the same efficiency as other foods. Ingestion losses from detrital DDT (M_{PD} in μg/d) were determined as

$$(13) \quad M_{PD} = M_D \cdot P_D / D$$

a calculation analogous to those used for organismic compartments (equation 8). The presence of a substantial detrital DDT compartment decreases DDT levels in the organisms in two ways: increasing the amount of ingested DDT also increases defecation and sedimentation losses of pesticide; and proportioning DDT over an additional compartment, the detritus, dilutes the remainder. This adjustment also removes most of the free DDT pool. Because free DDT is an important source for smaller organisms, this leads more rapidly to a more pronounced trend for body burden to increase with size (Table 3). Decreasing assimilation efficiency enhances this trend as does increasing loss rate.

The inclusion of excretion (Ep_i, in μg/d) as a negative term on the right-hand side of equation (6) had a substantial effect (Table 4). Pesticide excretion is assumed to be an allometric function of body size such that

$$(14) \quad Ep_i = P_i \cdot a\, W_i^b$$

where a and b are assumed constants which should eventually be replaced by empirically fitted values. Excreted pesticide was assumed to pass to the free pool from which it could be reabsorbed by the living community. If a 1-g animal loses 5% of its body burden daily ($a = 0.05$; Harding and Vass 1979) and loss is proportional to metabolic rate ($b = -0.25$), the model's results are little changed: values are lowered as more of the internal DDT is lost each day, especially for smaller organisms; but the same trends are obtained. If the value of a is decreased, the model approaches that with no excretion term. Increases of a above 0.05 lead to increasingly lower body burdens and slightly increased differences among size classes. These trends indicate that increasing loss of DDT removes somewhat more pesticide from small organisms. If one assumes that b, as the exponent of clearance, is -0.5 (Norstrom et al. 1976), then bioaccumulation is much more pronounced among larger animals. If clearance is unaffected by size ($b = 0$), small organisms accumulate the highest burdens. The overriding effects of the clearance function on patterns of bioaccumulation suggest that empirical determinations of this term are particularly important.

TABLE 3. The effect of the fate of defecated DDT on modeled patterns of bioaccumulation. Listed values are the body burdens in each size class 2 yr after delivery of a DDT pulse.

	Parameter			Size class				
	AB	*AE*	*L*	0.1	1.0	10	100	1000
1.[a]	0.75	0.9	0.5	1.14	1.18	1.23	1.23	1.07
2.	0.75	1.0	0.5	1.81	1.81	1.80	1.67	1.37
3.	0.75	0.9	0.5	0.73	0.78	0.86	0.91	0.82
4.	0.75	0.75	0.5	0.18	0.21	0.28	0.38	0.39
5.	0.75	0.9	0.1	0.87	0.91	0.99	1.02	0.91
6.	0.75	0.9	0.9	0.71	0.76	0.84	0.89	0.81

[a]Basic model: no detrital DDT.

TABLE 4. The effect of pesticide clearance on body burdens (μg/g) of different size classes 2 yr after delivery of a DDT pulse. The model in Fig. 1B has no excretion term and yields line 1. When an excretion function (equation 13) is added to the model, observed patterns are not markedly changed by variations in the intercept of the assumed relation (lines 2–4), but are strongly affected by changes in slope (lines 2, 5, and 6). Listed equations give the proportion of pesticide cleared daily. Other terms are defined in equations 1 to 12: $AB = 0.75$, $AE = 0.90$, $L = 0.5$.

		Size class				
	Clearance	0.1	1.0	10	100	1000
1.[a]	0	1.14	1.18	1.23	1.23	1.07
2.	$0.01W^{-0.25}$	1.14	1.17	1.21	1.26	1.25
3.	$0.05W^{-0.25}$	1.07	1.12	1.16	1.19	1.23
4.	$0.10W^{-0.25}$	0.96	1.06	1.11	1.15	1.18
5.	$0.05W^{-0.0}$	1.46	0.93	0.56	0.33	0.19
6.	$0.05W^{-0.5}$	0.59	1.11	1.84	2.85	3.87

[a]Basic model: no clearance.

Application of an Allometric Model

Testing of the hypothesis that body size influences bioaccumulation will require additional information and modification of the model presented above. First, allometric relations describing uptake and loss of a suitable contaminant must be experimentally determined. Studies for the flux of both natural materials (Brody 1964; Johannes 1964; Peters

1975) and contaminants (DiGregorio et al. 1978; Jorgensen 1979; Morgan 1964) have regularly reported marked size effects, and so it is probable that contaminant fluxes also scale to size. Application of the approach will also require measurement of the size frequency distribution of organisms in natural communities. The model generates a size frequency distribution which need not mimic those in nature. Measurement of size distribution appears tedious, but a number of automated devices exist which are capable of sensing the distribution of plankton (Sheldon and Parsons 1967), and imminent technological improvements may soon extend the range of automated surveys (Silvert and Platt 1978). The model also requires a detrital compartment to achieve mass balance and uses this to calculate an implicit mortality rate (equation 5) which, at equilibrium, scales as $W^{-0.25}$ (M_i/B_i, Table 1). In a natural system, this detrital pool will be difficult, if not impossible, to identify. Fortunately in application, explicit rates of mortality which are equal in magnitude but opposite in sign to production can instead be assigned to measured biotic compartments (Banse and Mosher 1980). The model's detrital compartment also serves as a recipient of fecal pesticide; in application this role will necessarily be assumed by a nonempirical utilization function which apportions fecal DDT to different compartments as we have no estimate of the scaling of coprophagy to size. Finally an empirical loss term must be introduced to replace the assumed loss rate in equation 11. Unless a mechanism for loss, such as net binding to inorganics or sedimentation, can be identified and quantified, an approximation must be sought by assigning observed rates of pesticide loss to fecal or free contaminant. As this term may depend on abiotic processes rather than on body size, its further development depends on the incorporation of physical or chemical models describing the half-life of pesticides in natural communities.

Because such a model describes the average behavior of all organisms of a given size, it is unlikely to predict body burden for a given target species of fish or pest. It may, however, describe the contaminant distribution in the environment of such a species. More detailed models (e.g. Norstrom et al. 1976) could then be coupled with this general model to treat specific cases. Similarly, it may be possible to imbed an allometric model in other physical or biotic models to yield predictions of burden within a limited range of size classes of fish or zooplankton.

Exercises with "reasonable assumptions" can be carried on indefinitely, and computer models only indicate logical possibilities within limits set by available data. In the present example, we show that qualitatively similar patterns of toxicant flow can be generated without recourse to food chains and trophic levels. Although food preferences could influence such patterns, and models which would combine trophic structure with allometric relations have an intuitive appeal, we believe that the identification of food webs in nature is impractically difficult and time-consuming. The model suggests that predictions can be achieved by considering the metabolic and physiological attributes of the organisms, but the current model is limited by the absence of empirical relations between body size and the uptake or release of pesticide. Nevertheless, this analysis indicates a direction for future experimentation which may provide a basis for quantitative prediction of ecological magnification.

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Lampetra macrostoma, a New Species of Freshwater Parasitic Lamprey from the West Coast of Canada

RICHARD J. BEAMISH

Department of Fisheries and Oceans, Resource Services Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

BEAMISH, R. J. 1982. ***Lampetra macrostoma***, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39: 736–747.

Lampetra macrostoma n.sp., a freshwater parasitic lamprey, is distinguished from related species *L. tridentata*, *L. lethophaga*, *L. folletti*, *L. minima*, and *L. similis* by its parasitic habit and very large disc. Other characters distinguishing the species from *L. tridentata* are its longer prebranchial length, large eye, weakly pigmented velar tentacles, and its ability to remain in freshwater. The recently metamorphosed form readily survives in freshwater and probably is non-anadromous even though it can survive in salt water. The new species has been discovered in two lakes on Vancouver Island, British Columbia, Canada, where it attacks large numbers of resident salmonids. Because of its ability to survive and feed in freshwater, it poses a definite threat to freshwater fishes.

Key words: lamprey, new species, non-anadromous lamprey, salmonid parasitism

BEAMISH, R. J. 1982. ***Lampetra macrostoma***, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39: 736–747.

Lampetra macrostoma n.sp., une lamproie parasite d'eau douce, se distingue des espèces apparentées *L. tridentata*, *L. lethophaga*, *L. folletti*, *L. minima* et *L. similis* par son mode de vie parasitaire et son disque buccal très grand. Les autres caractères qui différencient cette espèce de *L. tridentata* sont une longueur prébranchiale plus grande, un oeil plus grand, des tentacules vélaires faiblement pigmentées et sa capacité à demeurer en eau douce. La forme récemment métamorphosée survit facilement en eau douce et est probablement non anadrome, même si elle peut survivre en eau salée. La nouvelle espèce a été découverte dans deux lacs de l'île Vancouver, en Colombie-Britannique (Canada), où elle attaque de grands nombres de salmonidés résidants. Capable de survivre et de se nourrir en eau douce, l'espèce est une réelle menace pour les poissons d'eau douce.

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LAMPREYS possessing a supraoral lamina with 3 well-developed cusps, 4 innerlaterals on each side of the disc, and an infraoral lamina with 5 cusps (or a 3–4–5 formula) have been included in the genus *Entosphenus* by Gill (1862), Jordan and Evermann (1896), Berg (1931), Hubbs (1967), Vladykov and Follett (1965), McPhail and Lindsey (1970), and Vladykov and Kott (1976a). Others (Hubbs 1971; Hubbs and Potter 1971; Kan 1975) have combined this group with lampreys that have a supraoral lamina with 2 cusps, 3 innerlaterals on each side of the disc, and an infraoral lamina with 7 cusps (or a 2–3–7 formula) into the genus *Lampetra*. In this second system, *Entosphenus* may or may not be considered to be a subgenus of *Lampetra*. In this report, the genus *Lampetra* is used in the sense of Hubbs and Potter (1971) to conform with the terminology adopted by the American Fisheries Society (Robins et al. 1980). As more becomes known about the relationships of lampreys on the west coast of North America it is possible that the terminology of Vladykov and his co-workers will become popular again and the new species will be placed in the genus *Entosphenus*.

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The new species described in this paper belongs to the group with the 3–4–5 formula and is readily distinguished from the group with the 2–3–7 formula. Previously there were six known species that possess the 3–4–5 formula: *Lampetra tridentata*, *L. minima*, *L. similis*, *L. lethophaga*, *L. folletti*, and *L. hubbsi*. *Lampetra tridentata*, a parasitic species, was first described by Gairdner 1836 (in Richardson 1836, p. 293). *Lampetra minima* Bond and Kan, 1973 is a dwarfed parasitic derivative of *L. tridentata* that has been reported from only one lake and is now believed to be extinct; *L. minima* was distinguished from *L. tridentata* by its dwarfed size at maturity, a low number of trunk myomeres, the shape and number of the posterials, larger eye, a longer prebranchial region, and a paler, simpler coloration (Bond and Kan 1973). A third parasitic species, *L. similis* (Vladykov and Kott, 1979) differs from *L. tridentata* by having fewer velar tentacles and myomeres and a larger disc, and from *L. minima* by its larger size at maturity and its larger disc.

There also are three nonparasitic derivatives of *L. tridentata*. *Lampetra lethophaga* Hubbs, 1971, *L. folletti* (Vladykov and Kott, 1976b), and *L. hubbsi* (Vladykov and Kott, 1976c) are easily distinguished from the parasitic species by the nonfunctional digestive tract. *Lampetra letho-*

phaga frequently has a bicuspid supraoral lamina in addition to a tricuspid and a quadricuspid one (Hubbs 1971). The distinctions among these three non-parasitic species have been described by Vladykov and Kott (1976b, c).

It was not until the biology of adult and postlarval *L. tridentata* on the west coast of Canada was reexamined (R. J. Beamish 1980) that the very distinctive morphometric features of the new species were noted. At present the new species has been found in Lake Cowichan (124°17′W, 48°52.6′N) and the connected Mesachie Lake (124°07′W, 48°48.7′N) on Vancouver Island, British Columbia. The term non-anadromous rather than landlocked is used to describe the habit of this species as there currently are no physical barriers in these two lakes that prevent access to the sea.

Material and Methods

Postlarval or immature specimens were obtained using beach seines, purse seines, gill nets, traps, and from sports-caught fish that were landed with lamprey attached. Mature adults were trapped on a gravel bar at the inlet to Mesachie Lake. A 5-mm-square-mesh-galvanized wire fence was placed on the gravel bar at right angles to the shore. Unbaited minnow traps (mesh-covered cylinders of various sizes with conical entry tunnels at each end) were placed on the bottom along both sides and ends of the fence. Lamprey entered the openings of these traps apparently in an attempt to find passage around the fence.

Ammocoetes and recently metamorphosed individuals were collected using electroshockers in Mesachie Lake and Lake Cowichan. They were most plentiful along the edge of the lakes, rather than in outlet or inlet streams, and they were seldom found in any abundance.

Sixteen immature lamprey were obtained from Mesachie Lake in 1979 and 1 from Lake Cowichan in 1980. Ninety-four mature adults were captured from Mesachie Lake in 1980. Seventeen recently metamorphosed specimens were collected from Mesachie Lake in 1979 and maintained in the laboratory. A sample of 16 ammocoetes was examined from a collection made in Mesachie Lake during September 1979. A portion of the sample was kept alive using the procedures described in R. J. Beamish (1980).

Samples of *L. tridentata* were collected from two locations in British Columbia, Canada, for comparison with ***L. macrostoma*** n.sp. Between 1978 and 1980 one sample of 22 feeding adults was collected from the Strait of Georgia. All these lamprey were immature and were caught during research cruises or commercial fishery operations (R. J. Beamish 1980). A sample from Stamp River, collected at an artificial river bypass or fishway 14 km from the mouth of the river, was subsampled. The sample was obtained in June 1979 and consisted of individuals that had just entered freshwater prior to spawning in the spring of 1980. The gonads of all specimens were maturing. The body cavity of most juveniles was one third to about two thirds full of eggs, but there was no distention of the abdomen that is characteristic of females just prior to spawning.

Measurements and counts were made from the left side of specimens that had been previously preserved in 5% Formalin unless otherwise indicated. The procedures described by Vladykov and Follett (1965) were used. Tail length, trunk length, branchial length, prebranchial length, disc length, eye length, postorbital length, total length, and the height of the first and second dorsal fins were measured for each specimen. Myomeres were counted from the posterior branchial opening (first myomere not touching the posterior of the branchial opening) to the last myomere, whose lower posterior angle lies in part or wholly above the cloacal slit. Velar tentacles were examined and counted according to the procedures described by Vladykov and Kott (1979). Terminology used for the dentition was according to Vladykov and Follett (1967). All measurements except total length were expressed as a fraction of total lengths.

Experiments were conducted to compare the ability of recently metamorphosed ***L. macrostoma*** n.sp. and *L. tridentata* to remain in freshwater and to determine if feeding ***L. macrostoma*** n.sp. captured in a lake would acclimate and feed in full-strength seawater.

During September 1979, recently metamorphosed *L. tridentata* were collected from Robertson Creek (124°58.5′W, 49°19.8′W), Oyster River (125°07′W, 49°52.3′N), Qualicum River (124°37′W, 49°24′N), Haslam Creek (123°53′W, 49°04′N), and Babine Lake (126°W, 54°N). Recently metamorphosed ***L. macrostoma*** n.sp. were collected from Mesachie Lake in late September and early October 1979. At the end of September, five *L. tridentata* from each location were held in an 800-L tank with flowing freshwater of ambient temperature. A second similar experiment contained 48 *L. tridentata* with a minimum of 5 from each location. Five ***L. macrostoma*** n.sp. were added to the second experiment in November and five were held separately in a third tank. Small salmonids were maintained in all tanks for food for the duration of the experiments, except that all fish were removed from the first experiment at the end of October to determine if there might be some relationship between the presence of the fish and the observed lamprey mortalities.

In two other experiments, 37 and 40 recently metamorphosed *L. tridentata* from the same five locations were maintained in 800-L tanks in freshwater until mid-October and mid-November, respectively, when they were converted to full-strength salt water over a 3-d period. No salmonids were provided for food while lamprey were in freshwater.

In late September 1979, five recently metamorphosed ***L. macrostoma*** n.sp. were gradually introduced into full-strength salt water over a period of 3 d. This experiment was repeated on November 3 with an additional two lamprey. In December 1980, the experiment was repeated again, this time using four recently metamorphosed ***L. macrostoma*** n.sp.

In all experiments, freshwater was dechlorinated City of Nanaimo water; salt water was obtained directly from the Strait of Georgia and ranged in salinity from 27 to 30‰. Saltwater and freshwater ambient temperatures ranged from 8.5 to 10.5°C and 4.5 to 11.5°C, respectively, during the experiment. Photoperiod was not regulated, and tanks were darkened with opaque plastic covers.

Results and Discussion

Lampetra macrostoma n.sp.

SYNONYM: *E. tridentatus*; of Carl (1953).

ETYMOLOGY: The specific name in Latin means large opening

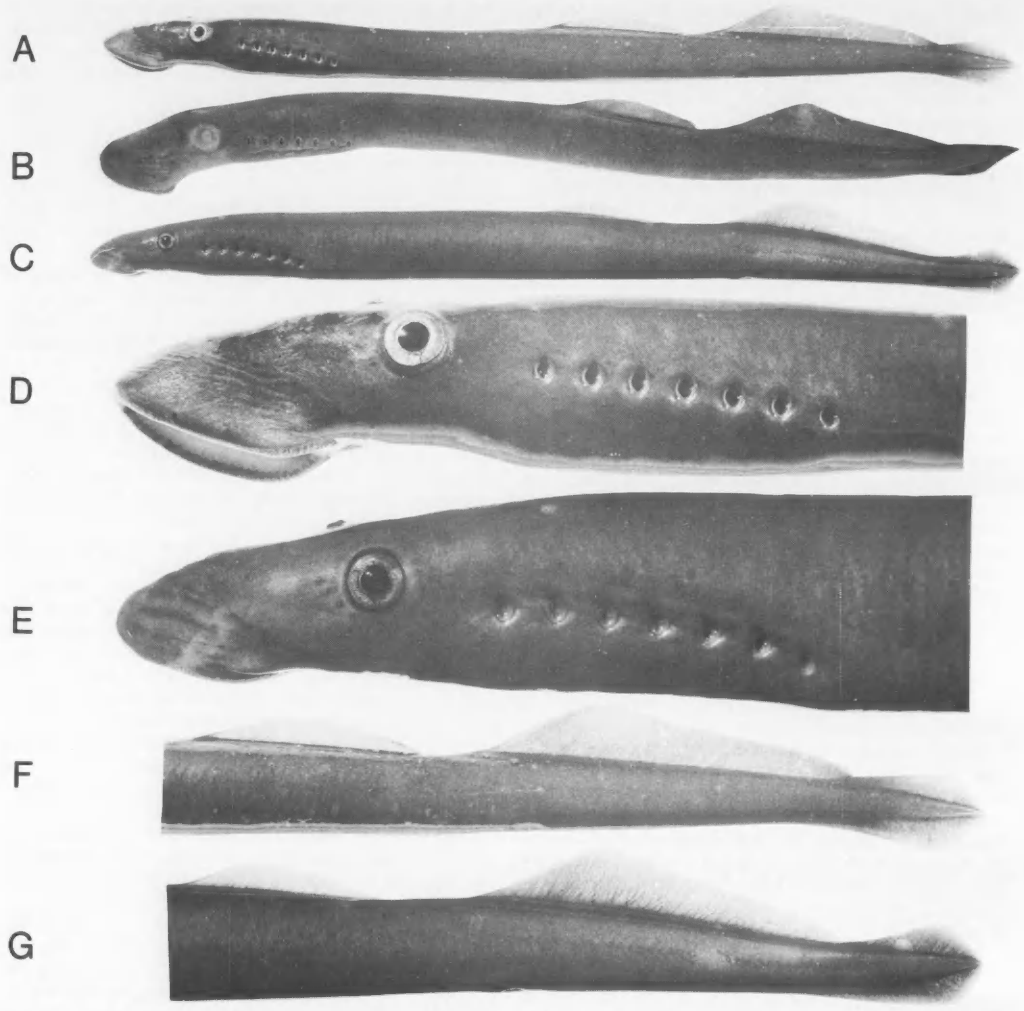

FIG. 1A. Lateral view of the holotype of *L. macrostoma*. B. Holotype after preservation. C. Lateral view of *L. tridentata* (29.0-cm specimen from the Qualicum River. D. Head region of holotype. E. Head region of *L. tridentata* in C. F. Tail region of holotype. G. Tail region of *L. tridentata* in C. All photographs were of live specimens except B.

in reference to the very large disc or mouth, compared to *L. tridentata*.

COMMON NAME: Lake lamprey.

HOLOTYPE: National Museum of Natural Sciences, Ottawa, Canada, No. NMC 81-1219 caught November 14, 1980 in Lake Cowichan, Vancouver Island, British Columbia, attached to a coho salmon (*Oncorhynchus kisutch*).

DESCRIPTION OF HOLOTYPE

Immature male; 22.8 cm total length before preservation (Fig. 1A) and 22.1 cm after preservation (Fig. 1B); preserved weight 19.8 g; preserved measurements (as % TL); tail length 28.8, trunk length 42.4, branchial length 10.8, prebranchial length 15.9, disc length 10.0, eye diameter 2.7, postorbital length 2.7, height of first dorsal fin 2.0, height of second dorsal fin 4.2; supraoral lamina tricuspid. Four inner lateral teeth on each side of disc, first and fourth bicuspid, second and third tricuspid. Infraoral lamina with 6 cusps. Anterials 10, posterials 18. Three anterior posterials on each side of disc bicuspid. Marginals 62. Transverse lingual lamina with 17 cusps, median cusp slightly enlarged. Left longitudinal lingual lamina with 27 cusps. Velar tentacles 14, and myo-

meres 64.

The new species is known to reside in lakes and probably is non-anadromous even though it can survive in salt water.

PARATYPES

All mature males and females were in spawning condition and were collected by Messrs Mike Smith, Ed Pawlik, John Richards, and myself from a gravel bar in Mesachie Lake from June 1 to August 23, 1980. The sample consists of 53 males and 41 females ranging in length from 17.9 to 25.6 cm. National Museum of Natural Sciences, Ottawa, Canada, No. NMC 81-1220. A sample of 16 immature fish that were collected in 1979 from Mesachie Lake are catalogued as NMC

TABLE 1. Proportional measurements (% TL), number of cusps, velar tentacles, and myomeres from lamprey examined in this and other studies. Range in parentheses.

	L. macrostoma mature	*L. macrostoma* immature	*L. tridentata* maturing,[c] Stamp River	*L. tridentata* immature, St. of Georgia	*L. minima*, Miller Lake, Oregon[d,e]
Total length (TL), cm	20.6 (17.9–25.6)	17.4 (11.8–27.3)	28.6 (24.5–32.1)	25.1 (18.4–33.1)	8.5 (7.2–12.9)
Tail length	28.4 (20.9–31.7)	27.9 (25.7–30.8)	28.4 (24.9–30.1)	26.7 (23.6–28.5)	30.7 (25.9–32.9)
Trunk length	42.3 (37.5–48.2)	42.6 (38.0–46.1)	45.2 (42.1–48.5)	46.7 (43.0–54.0)	45.2 (42.6–51.3)
Branchial length	11.0 (10.0–12.6)	10.5 (9.4–11.1)	10.7 (9.0–11.4)	10.4 (9.6–11.3)	9.2 (7.9–10.8)
Prebranchial length	15.9 (15.2–17.2)	15.4 (14.3–17.6)	13.1 (12.4–13.9)	13.9 (10.9–15.7)	14.8 (13.4–16.4)
Disc length	10.0 (6.5–11.7)	9.7 (8.8–11.4)	7.3 (6.4–8.2)	7.1 (4.6–9.1)	6.2 (5.0–7.4)
Eye diameter	2.8 (2.4–3.5)	2.9 (2.2–3.3)	2.2 (1.9–2.6)	2.5 (1.9–3.2)	2.4 (2.1–3.1)
Postorbital length	2.8 (2.3–4.4)	2.7 (2.5–3.1)	2.8 (2.5–3.2)	2.8 (2.2–3.4)	—
Height of 1st dorsal fin	3.1 (2.2–4.1)	1.9 (1.3–2.4)	2.2 (1.7–2.8)	2.0 (1.4–2.7)	—
Height of 2nd dorsal fin	4.7 (2.6–6.5)	3.3 (2.2–4.2)	3.6 (2.9–4.1)	4.0 (2.6–4.8)	5.0 (4.4–6.1)
No. myomeres	65.1 (62–70)	64.9 (59–68)	65.2 (63–69)	65.2 (60–70)	63.8 (62–65)
No. velar tentacles	13.4 (11–15)	13.2 (11–14)	13.8 (13–17)	14.1 (12–16)	6.3 (5–7)
Supraorals	3.0	3.1 (3–4)	3.0	3.0	3.0 (2–3)
Innerlaterals[a]	2–3–3–2	2–3–3–2	2–3–3–2	2–3–3–2	2–3–3–2
Infraorals	5.1 (5–6)	5.3 (5–6)	5.1	5.0	5.0 (5)
Anterials	8.8 (6–12)	9.9 (8–11)	8.0	8.2 (6–12)	7.1 (6–10)
Posterials	18.1 (16–21)	17.8 (14–21)	17.2	17.1 (16–19)	14.4 (11–17)
Marginals	59.7 (54–67)	—	54.0 (48–60)	54.4 (49–62)	—
Transverse lingual lamina	15.5 (13–19)	16.1 (13–20)	16.1	17.5 (16–20)	25.6 (20–29)
Longitudinal lingual lamina	22.2 (17–25)	23.8 (22–26)	21.0	24.2 (22–27)	22.1 (18–25)
Number examined[b]	94	17	30	22	45

	L. similis,[c] Klamath River		*L. tridentata*[f]		*L. tridentata*,[c] Sprague River, landlocked
	<17.0 cm	17–30.0 cm	Upper Klamath Lake	Pacific Ocean, immature	
Total length (TL) cm	14.7 (13.6–16.3)	22.6 (18.8–26.9)	22.4 (16.1–29.4)	21.0 (18.5–29.2)	25.9 (22.5–28.4)
Tail length	31.8 (30.2–34.9)	29.0 (27.0–32.1)	30.6 (29.2–31.9)	27.8 (24.6–29.6)	32.3
Trunk length	44.7 (42.5–47.8)	47.2 (44.9–52.0)	46.3 (44.2–48.4)	48.1 (43.4–51.6)	46.1
Branchial length	9.2 (8.2–10.6)	9.9 (8.5–11.8)	9.7 (8.6–10.3)	9.7 (8.6–10.3)	9.8
Prebranchial length	15.0 (14.4–16.4)	14.3 (13.0–15.6)	13.4 (12.0–14.6)	13.8 (12.0–16.0)	12.2
Disc length	9.0 (8.5–10.3)	9.3 (7.8–10.4)	6.7 (6.1–7.4)	6.1 (5.0–6.8)	6.6
Eye diameter	2.4 (2.0–2.7)	2.0 (1.4–2.4)	1.7 (1.3–2.0)	2.5 (1.9–3.7)	2.0
Postorbital length	—	—	—	—	—
Height of 1st dorsal fin	—	—	—	—	—
Height of 2nd dorsal fin	—	—	2.8 (2.2–3.2)	3.3 (2.5–5.8)	—
No. myomeres	61.5 (58–65)		63.1 (59–66)	—	64.7 (63–66)
No. velar tentacles	8.0 (7–9)		6.1 (6–8)	—	9.0 (7–11)
Supraorals	3.0 (3)		—	—	3.0
Innerlaterals[a]	2–3–3–2		—	—	2–3–3–2
Infraorals	5.2 (5–6)		—	—	5.2 (5–6)
Anterials	12.8 (10–15)		—	—	14.5 (12–17)
Posterials	18.0 (16–20)		—	—	18.0 (16–20)
Marginals	—		—	—	—
Transverse lingual lamina	22.9 (20–29)		(18–21)	—	19.1 (16–23)
Longitudinal lingual lamina	28.1 (24–33)		(24–28)	—	23.8 (20–26)
Number examined[b]	22		39	12	14

TABLE 1. (*Concluded*)

	L. tridentata,[c] Cultus Lake, landlocked	*L. tridentata*[e] maturing		
		<17 cm	17–30 cm	>30 cm
Total length (TL) cm	20.6	12.6 (9.6–15.9)	24.5 (19.2–30.0)	50.5 (31.2–71.6)
Tail length	28.2	29.9 (26.8–34.9)	29.7 (25.9–31.3)	30.7 (25.6–32.1)
Trunk length	45.2	45.8 (40.3–50.4)	45.9 (42.9–49.3)	47.1 (42.6–50.3)
Branchial length	11.3	9.6 (7.8–12.0)	11.2 (10.3–12.3)	11.0 (9.7–12.3)
Prebranchial length	15.6	14.8 (13.0–18.0)	13.4 (12.1–14.6)	12.1 (9.8–14.5)
Disc length	8.2	7.0 (4.7–8.5)	6.8 (6.0–7.8)	6.2 (4.7–8.0)
Eye diameter	3.4	3.7 (2.4–4.5)	2.6 (2.0–3.1)	1.8 (1.3–2.7)
Postorbital length	—	—	—	—
Height of 1st dorsal fin	—	—	—	—
Height of 2nd dorsal fin	—	—	—	—
No. myomeres	66.3 (65–69)		67.8 (62–71)	
No. velar tentacles	12.6 (11–14)		13.4 (10–17)	
Supraorals	3.0		3.0	
Innerlaterals[a]	2–3–3–2		2–3–3–2	
Infraorals	5.0 (5–6)		5.0 (5–6)	
Anterials	17.6 (5–10)		8.3 (5–11)	
Posterials	17.5 (14–19)		17.8 (12–21)	
Marginals	—		—	
Transverse lingual lamina	17.9 (16–19)		17.9 (14–21)	
Longitudinal lingual lamina	—		22.3 (20–24)	
Number examined[b]	14	90	20	30

[a]Typical formula.
[b]Numbers examined in this study refer to all measurements; however, in other studies, numbers of specimens used for counts are usually less than the number indicated.
[c]Collected during upstream migration in freshwater in June 1979.
[d]Bond and Kan (1973.)
[e]Teeth and velar tentacle counts from Vladykov and Kott (1979).
[f]Kan (1975).

TABLE 2. Comparison of disc lengths of recently metamorphosed *L. macrostoma* and *L. tridentata* sampled in December 1980.

	Total length (cm)	Disc length/ total length	No.
L. macrostoma (Mesachie Lake)	12.3	0.8	7
L. tridentata (Robertson Creek)	11.9	0.6	4

81-1221 and one immature lamprey from Lake Cowichan collected in 1980 is catalogued as NMC 81-1222.

METAMORPHOSED SPECIMENS

Total length (Table 1) — Spawning males and females 20.6 cm (17.9–25.6 cm), immature specimens 17.4 cm (11.8–27.3 cm); five recently metamorphosed specimens collected in Mesachie Lake in September 1979 12.3 cm (11.8–13.9 cm).

Body proportions (Tables 1, 2, 3) — Average measurements (% TL) similar for mature and immature specimens except for the higher dorsal fins of mature fish (Table 1): average measurements expressed as percentage of total length similar for immature males and females (Table 3); mature females had shorter tail length, longer trunk length, and slightly shorter branchial length, prebranchial length, disc length, and higher second dorsal fin than males (Table 3). For average measurements in percentage of the total length, first number refers to mature specimens and second number to immature specimens (Table 1): tail length 28.4, 27.9; trunk length 42.3, 42.6; branchial length 11.0, 10.5; prebranchial length 15.9, 15.4; disc length 10.0, 9.7; eye diameter 2.8, 2.9; postorbital length 2.8, 2.7.

Trunk myomeres (Tables 1, 3) — 65.1 (59–70).

Velar tentacles (Tables 1, 3) — Long and slender with lateral tentacles curving onto dorsal surface: number ranged from 9 to 15 with averages of 13.4 for mature specimens and 11.5 for immature specimens: lower number for immature specimens probably results from difficulties associated with identifying some of the smaller tentacles: base and lower portion of tentacles weakly pigmented.

Dentition (Table 1, Fig. 2E) — Transverse lingual lamina with 13–19 cusps, median cusp enlarged; paired longitudinal lamina with 17–25 cusps; supraoral lamina almost always tricuspid, without exception 4 inner laterals on each side with a cusp formula of 2–3–3–2; infraoral lamina usually 5 cusps but occasional specimen with 6 cusps, all cusps prominent and well developed; 16–21 posterials, outer 3 on each side

TABLE 3. Body proportions (% TL), myomere, and velar tentacle counts of immature and mature male and female *L. macrostoma* (range in parentheses).

	Immature		Mature	
	Male	Female	Male	Female
Total length (TL) cm	17.9 (12.0–23.6)	18.9 (11.8–27.3)	21.1 (17.9–27.2)	20.4 (18.2–25.6)
Tail length	27.7 (26.1–29.2)	28.8 (26.2–30.8)	29.7 (26.9–31.7)	26.8 (20.9–31.5)
Trunk length	42.4 (41.2–44.6)	42.5 (39.9–44.4)	40.4 (37.5–44.0)	44.7 (39.0–48.2)
Branchial length	10.6 (9.8–11.1)	10.4 (9.9–10.9)	11.4 (10.0–12.6)	10.6 (6.9–11.9)
Prebranchial length	15.8 (17.0–14.6)	15.7 (15.0–16.5)	16.1 (15.2–17.2)	15.5 (14.2–17.2)
Disc length	9.7 (8.8–11.4)	9.6 (9.0–10.4)	10.3 (8.1–11.8)	9.6 (6.5–11.7)
Eye diameter	2.9 (2.5–3.3)	2.9 (2.2–3.4)	2.7 (2.4–3.0)	2.9 (2.6–3.5)
Postorbital length	2.7 (2.6–3.0)	2.7 (2.5–2.9)	2.8 (2.3–3.2)	2.9 (2.5–4.4)
Height of 1st dorsal fin	1.9 (1.4–2.3)	2.0 (1.5–2.3)	3.2 (2.2–3.9)	3.1 (2.2–4.1)
Height of 2nd dorsal fin	3.5 (2.3–4.2)	3.5 (2.2–4.4)	4.6 (2.6–5.5)	5.1 (3.8–6.5)
Myomeres	64.3 (59–68)	66.3 (64–69)	64.5 (62–67)	65.9 (63–70)
Velar tentacles	13.1 (11–14)	13.3 (13–14)	13.3 (11–15)	13.6 (11–15)
Number examined[a]	10	5	53	41

[a]Sex of some immature individuals could not be determined.

bicuspid; anterials averaged ~ 9 and ranged 6–12 for all specimens and 9–11 for immature specimens, only the counts of immature specimens were considered to be reliable as some mature specimens lost anterials when touched; 54–67 marginals, easily separated from anterials except in extreme anterior field.

Color (Fig. 1, 2) — Specimens uniformly dark, almost black; both dorsal fins pigmented, although second dorsal fin more heavily pigmented; caudal fin pigmented but flesh above notochord clearly identifiable (Fig. 1A, F, 2C, 3B) and uniformly pigmented.

Sexual dimorphism — Males readily identifiable by presence of an external genital papilla.

Comparisons — Postlarval individuals of *L. macrostoma* are readily distinguished from nonparasitic species by their functional digestive tract and prominent dentition. They differ from the parasitic species that have a supraoral lamina with 2 well-developed cusps, 3 inner laterals on each side of the disc, and an infraoral lamina with 7 cusps in having a supraoral lamina with 3 cusps, 4 innerlaterals on each side of the disc and 5 cusps on the supraoral lamina. Mature individuals were smaller than the average *L. tridentata* from a number of other locations in British Columbia (R. J. Beamish 1980, Table 1), but were larger than the dwarf *L. minima* (Table 1). Sizes were similar to *L. similis*, a subspecies of *L. tridentata* proposed by Kan (1975) and some other populations of reportedly non-anadromous *L. tridentata* (Table 1).

Lampetra macrostoma has a large disc (Fig. 2A, C, E) that is considerably bigger than the discs of *L. tridentata* from the Stamp River, the Strait of Georgia (Table 1), or the Qualicum River (Fig. 2B, D). The flattened disc of *L. macrostoma* (Fig. 2A) has approximately two thirds more surface area than the disc of similar size *L. tridentata* (Fig. 2B). The characteristically large size of the disc readily visible on fresh and preserved specimens (Fig. 1A, B, D) in adult, recently metamorphosed and immature specimens (Fig. 3A, B, Table 2), is the key character distinguishing *L. macrostoma* from *L. tridentata*. The large disc results in relatively large wounds on hosts (Fig. 3G) that can be mistakenly interpreted as attacks by very large *L. tridentata* on small fish.

Lampetra macrostoma has a large eye, a longer prebranchial length, and possibly a shorter trunk length compared to the *L. tridentata* examined in this study (Table 1, Fig. 1D, E).

Lampetra macrostoma differs from *L. minima* primarily by the much larger disc and greater number of velar tentacles. It also is larger at maturity, has a larger eye, fewer transverse lingual laminae, and possibly a shorter trunk length and a longer branchial length. It differs from *L. similis* primarily by the larger number of velar tentacles, but it also appears to have a shorter trunk length, longer branchial length, and a slightly larger eye and disc. The prebranchial appears slightly longer, and there may be more myomeres and fewer cusps on the transverse and longitudinal lingual lamina.

Lampetra macrostoma can be distinguished from a subspecies of *L. tridentata* (Kan 1975) by the larger disc, larger eye, and greater number of velar tentacles. *Lampetra macrostoma* also appears to have a larger prebranchial, shorter trunk and longer branchial region. It is interesting that the major difference between this subspecies identified by Kan (1975) and *L. similis* is the size of the disc (Table 1).

When *L. macrostoma* is compared to samples of *L. tridentata* examined in other studies, the size of the disc remains distinctive. A sample from Cultus Lake that Vladykov and Kott (1979) claimed was landlocked appears similar to *L. macrostoma* although the disc size remains smaller. The larger disc and greater number of velar tentacles separated *L. macrostoma* from a sample of "landlocked *L. tridentata*" described by Vladykov and Kott (1979) from the Sprague River.

It is interesting to note that the major differences between *L. minima* and *L. similis* are the size at maturity and disc size. Because size at maturity is quite variable for other species of fishes (Beamish and Crossman 1977), the size of the disc becomes a principal character for separating these species. Vladykov and Kott (1979) also concluded that disc size was an important character and stated "the principal differences

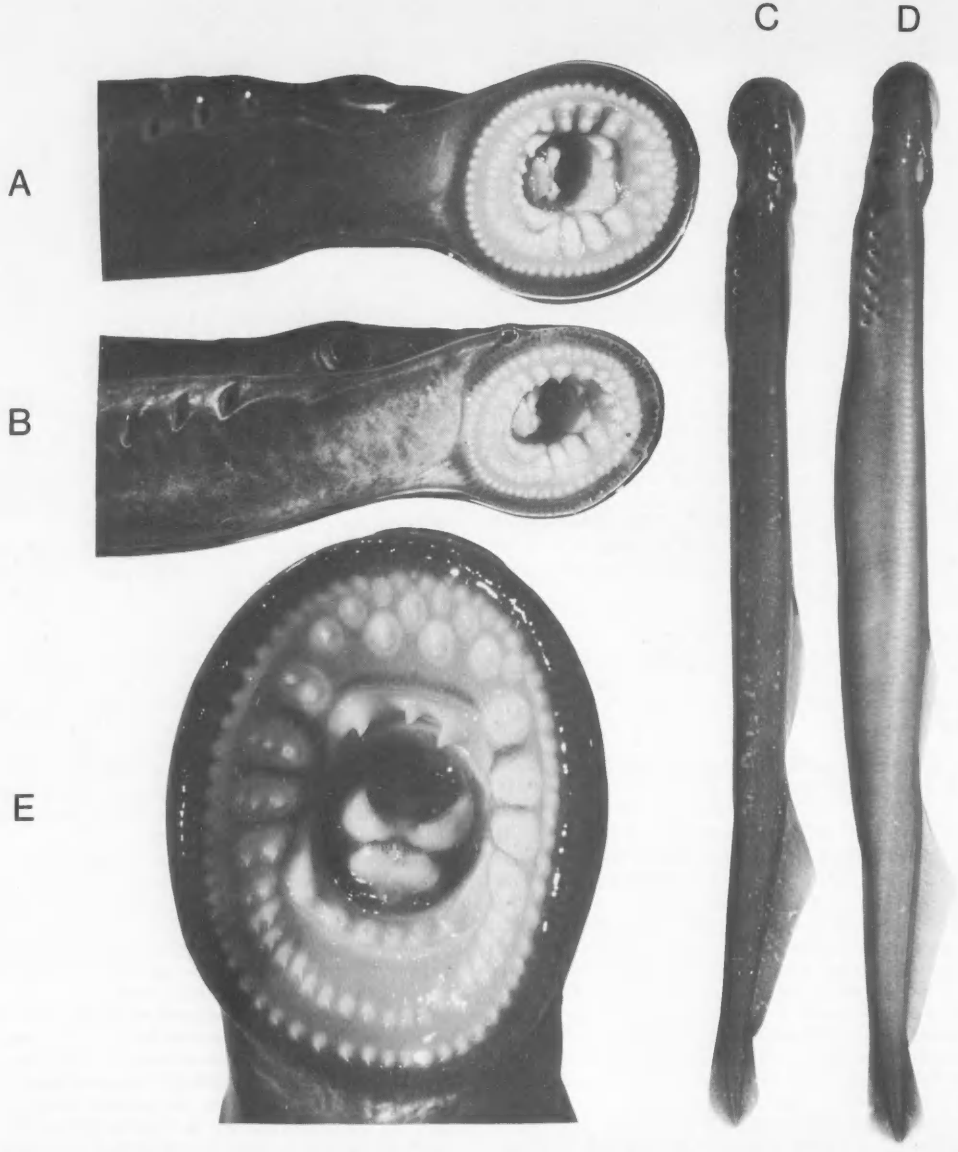

FIG. 2A. Ventral view of holotype. B. Ventral view of *L. tridentata* in Fig. 1. C. Dorsal view of holotype. D. Dorsal view of *L. tridentata* in B. E. Ventral view of disc of holotype. All photographs were of live specimens.

between the parasitic species of *Entosphenus* are in the length of the disc and eye, which are proportionately larger in smaller specimens."

The number of velar tentacles is a useful character for separating species (Table 1). Because of the range in counts in *L. macrostoma*, the number of velar tentacles must be considered to be similar to the number observed for *L. tridentata* (Table 1). There was no obvious difference in the shape of the velar tentacles; however, those of *L. macrostoma* were very weakly pigmented relative to the darkly pigmented

base and lower portion of the velar tentacles of *L. tridentata*.

There were apparent differences in dentition among some species in Table 1 such as the higher number of cusps on the traverse lingual lamina for *L. minima* and *L. similis* and possibly a higher number of cusps on the longitudinal lingual lamina for *L. similis*. *Lampetra minima* appears to have fewer posterials, and *L. similis* and the Sprague River landlocked form in Oregon has a greater number of anterials.

Mature *L. macrostoma* males had a larger disc than females, but the eye and second dorsal were slightly smaller. Females had a greater trunk length, but males had a larger tail length. If females decrease in size during maturation more than males as found for other species (F. W. H. Beamish 1980; R. J. Beamish 1980), then the body proportions of females (% TL) might be expected to be greater for mature females than males because they were similar as immature individuals (a comparison of immature males and female fish (Table 3) indicated there was little difference in body proportions). Because there was no consistent trend in changes of body proportions of females, it appears that allometric shrinkage occurs in males and females during maturation.

Ammocoetes

The sample of 16 ammocoetes examined for body proportions has the National Museum of Natural Sciences No. NMC 81-1223. Body proportions (% TL): tail length 30.0 (28.3−33.1), trunk length 47.8 (45.5−51.4), branchial length 14.4 (12.8−15.7), prebranchial length 9.2 (7.6−10.7), disc length 5.1 (4.8−6.6). Myomere counts averaged 66.1, which is slightly higher than the average of ~ 65 found in this study for adult *L. tridentata* and *L. macrostoma* and slightly lower than the average of 67.5 found for ammocoetes of *L. tridentata* by Pletcher (1963).

The pigmentation of the branchial region from preserved specimens (Fig. 3C) was similar to that reported for ammocoetes of *L. folletti*, *L. lethophaga*, and *L. minima* (Vladykov and Kott 1976b), but not for *L. tridentata* (Vladykov and Kott 1976b; Pletcher 1963). Both Pletcher and Vladykov reported that the latter has a patch of unpigmented area above the first branchial pore. Pletcher showed that the pigmentation extends close to the other branchial pores and Vladykov showed that *L. tridentata* ammocoetes have a broad band of unpigmented area above the branchial pores. The ammocoetes examined in this study did not have a clear patch above the first branchial pore, and a nonpigmented area above the branchial pores was absent (Fig. 3C, D). Despite the differences in the branchial region pigmentation of *L. macrostoma* and *L. tridentata*, the head pigmentation pattern is not characteristic of this new species because there are important variations in the pattern reported for *L. tridentata* (Vladykov and Kott 1976b; Pletcher 1963). The pigmentation of the head region of living specimens (Fig. 3D) was much darker, and it was difficult to identify a clear pattern.

The pigmentation of the tail region (Fig. 3E, F) was similar to the pigmentation of the *L. tridentata* ammocoete shown, but not described in Vladykov and Kott (1976b). We have found that the pigmentation of the tail region is the only method for distinguishing live and preserved ammocoetes of *L. tridentata* and its derivatives in British Columbia (Richards 1980). The pattern also is similar to the pattern shown for *L. tridentata* derivatives (Vladykov and Kott 1976b). The area above the notochord in the caudal fin is uniformly lightly pigmented, often grayish. The dorsal and ventral edge of the caudal ridge has a thin dark band, and the caudal fin is deeply pigmented immediately adjacent to the ridge (Fig. 3E, F). In living specimens (Fig. 3F) the dark bands are accentuated by areas of reduced pigmentation immediately to the interior. The pigmentation in the caudal fin may extend for varying distances, but usually extends about halfway to the edge of the fin. This pattern is readily distinguished from the dark caudal area found on *L. richardsoni* Vladykov and Follett, 1965 and *L. ayresi*.

The bulb of the tongue precursor of *L. macrostoma* is unpigmented, and there is little or no black pigmentation on either side of the elastic ridge. The pigmentation is similar to the tongue precursor shown for *L. tridentata* in Vladykov and Kott (1976b).

Part of the sample collected in September 1979 was kept alive and fed (R. J. Beamish 1980). Four of the larger ammocoetes metamorphosed, and all were *L. macrostoma*. In 1980, a sample of 227 ammocoetes from Lake Cowichan was kept alive and fed. In October 1981, 59 of these had metamorphosed, and all were *L. macrostoma*. Because subsamples of these two samples were preserved and examined in this study, it is probable that they were *L. macrostoma*. Ammocoetes of *L. macrostoma* ranging from 1.6 to 17.0 cm have been found in Lake Cowichan and Mesachie Lake. The larger ammocoetes (10−17 cm) are not unusual in the areas where ammocoetes occur.

Biology

The life history of this new species is currently being examined. Preliminary results indicate that adults spawn on shallow gravel bars in the lake. Mature males and females in spawning condition have been captured from May to August at two sites, and it is assumed that spawning would occur over this period. Ammocoetes were found primarily in the silt bottom of the lake or in the inlet of streams that flowed into the lake. Few were found at distances greater than 100 m from the lake, indicating that the lake is the principal rearing area for larvae. At this time nothing is known about their depth distribution or the average duration of ammocoete life.

Metamorphosing lamprey have been collected in the two lakes from mid-September until mid-November. The stage of metamorphosis was not as advanced as that of *L. tridentata* collected over the same period from other areas.

Feeding adults readily attack resident fishes. Up to 50% of fish collected throughout the year had some evidence of being attacked by lamprey. In one sample of 221 salmonids, 15% had wounds that penetrated the body cavity (Fig. 3G) or penetrated deeply into the muscle and probably would result in the death of the fish. Carl (1953) reported that 8 of 10 fish examined from Lake Cowichan had been attacked by lamprey. During the summer of 1980, coho salmon that were killed by lamprey were found on the bottom of the lake and washed up along the shore. There was no doubt that this species was a serious predator of resident fishes and an important source of mortality.

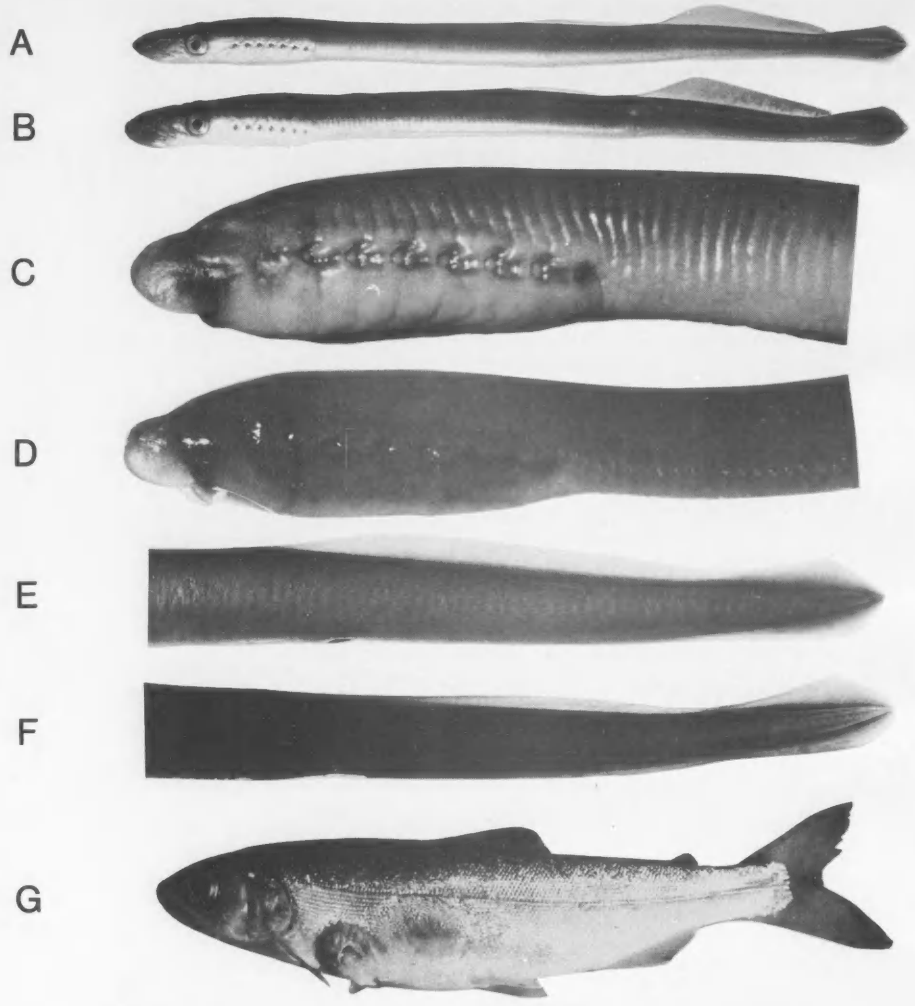

FIG. 3A. Recently metamorphosed live *L. tridentata* from the Stamp River (11.5 cm). B. Recently metamorphosed live *L. macrostoma* from Mesachie Lake (12.0 cm). A and B were photographed in December 1980. C. Anterior of preserved *L. macrostoma* ammocoete (11.4 cm). D. Anterior of live *L. macrostoma* ammocoete from Mesachie Lake (12 cm). E. Tail region of ammocoete in C. F. Tail region of ammocoete in D. G. *Lampetra macrostoma* wound on 19-cm salmonid found dead on the bottom of Mesachie Lake.

The duration of adult life is unknown. It is suspected that postlarval lamprey may begin to feed in the spring following metamorphosis. Feeding continues throughout the year as evidenced by the fresh wounds that were observed on prey throughout the year. Thus the minimum length of life from onset of metamorphosis to death following spawning is 2 yr, but the actual life span probably is longer. All mature adults held in the laboratory died after spawning.

PHYSIOLOGY

When recently metamorphosed *L. macrostoma* were held in freshwater separately and with samples of recently metamorphosed *L. tridentata* from five locations, all *L. macrostoma* survived while 50% of the *L. tridentata* died before the end of November, and none survived past March of the next year (Fig. 4). Both freshwater holding experiments with

L. tridentata produced similar results (Fig. 4). In both experiments feeding was initiated in mid-October. While the cause of death of *L. tridentata* was not determined, there can be no question that *L. macrostoma* was better adapted than *L. tridentata* to survive in freshwater in these experiments. This suggests that the non-anadromous habit of *L. macrostoma* is distinct from the anadromous habit of *L. tridentata*.

In contrast to the total mortality observed for *L. tridentata* in freshwater, there was very little mortality of *L. tridentata* from the same locations once they were acclimated to salt water. In one experiment (Fig. 4, experiment 4) there was an initial death in freshwater; however, there were no deaths from mid-October until shortly after conversion to salt water in mid-November (Fig. 4). After these initial deaths in salt water, no others were observed. These lamprey were maintained in salt water, and many were still alive in December 1981. In experiment 5 in which *L. tridentata* were introduced into salt water in October, there were 10 deaths during conversion, and 2 a few days after full-strength salt water was reached (Fig. 4). There were two deaths in mid-February, and no more mortality until the end of the experiment in March 1980. The deaths during the conversion to salt water probably resulted from forcing the lamprey into full-strength salt water before metamorphosis was completed (Richards 1980). After March 1980 these lamprey were maintained and fed in salt water, and many were still alive in December 1981.

The lamprey held in freshwater in experiment 4 until mid-November (Fig. 4) did not suffer similar mortality rates as the lamprey held in the two freshwater holding experiments. Because the only known difference among these experiments was that the lamprey converted to salt water were not fed while in the other two experiments fish were supplied and feeding commenced in mid-October, it is possible that the rate of mortality in freshwater was related to the onset of feeding. Because the removal of fish at the end of October did not affect the rate of mortality, any relationship may be to the onset, and not the amount, of feeding.

In the final experiments in which five *L. macrostoma* were subjected to increasing concentrations of salt water with five *L. tridentata* from five locations, all died within 3 d while 80% of the *L. tridentata* survived and remained feeding in salt water. The cause of death of all lamprey appeared to be related to the stage of metamorphosis. Those that died had not reached stage 6 or had just reached stage 6 (Richards 1980). On November 3, 1979, an attempt was made to acclimate two more recently metamorphosed *L. macrostoma* to salt water. One died within 2 d (~20‰) and the other survived. In December 1980, four recently metamorphosed *L. macrostoma* were acclimated to full-strength salt water over a 3-d period; two died in the summer of 1981 and two were maintained until November 1981 when the experiment was terminated. The two that remained grew from an average size of 9.5 cm and 1.5 g to 22.8 cm and 11.5 g in 11 mo. It appeared that *L. macrostoma* will not survive in salt water as early as *L. tridentata*, but will acclimate with little difficulty a few months later.

In June 1979, two feeding adult *L. macrostoma* were captured in Mesachie Lake and gradually acclimated to full-strength salt water over a period of 3 d. In November 1979, two feeding adults were captured in Mesachie Lake and acclimated to full-strength salt water over a period of 3 d and maintained in salt water with salmonids used as food. In both experiments the lamprey were probably in their second post-larval year, again indicating that *L. macrostoma* can live and feed in salt water.

Conclusions

Lampreys, which are believed to be at least 280 million yr old, are one of the most primitive groups of living fishes and have few characters that can be used for taxonomy. Dentition characters are used for generic level distinctions (Berg 1940; Vladykov and Follett 1967), and morphological characters along with trophic or life history distinctions form the basis for species or subspecies distinctions (Hubbs and Potter 1971). Often the distinctions may appear trivial and not of sufficient importance to warrant a species designation. For example, the distinction between *L. ayresi* and *L. fluviatilis* (cf. Vladykov and Follett 1958) (expressed as % TL) is based on one species having a larger eye (3.3 compared to 2.2), a larger prebranchial length (12.5 compared to 11.6), and a shorter branchial length (9.0 compared to 10.0). The differences in these body proportions are similar to differences described in Table 1 and may appear of minor significance; however, Hubbs and Potter (1971) heralded this separation as "one of the highlights in clarifying lamprey systematics."

The distinctions separating *L. similis*, *L. minima*, and *L. tridentata* similarly may appear of minor importance, yet these lamprey have been accepted as distinct species. Vladykov and Kott (1979) believe that the disc is "the distinctive character separating species of parasitic lamprey," and it is the size of the disc of *L. macrostoma* that distinguishes it from *L. tridentata*. Therefore, apparently minor differences are considered important, and differences in the size of the disc and eye, prebranchial lengths, and pigmentation of the velar tentacles are sufficient to allow *L. macrostoma* to be called a new species; certainly it is as distinctive as the other derivatives of *L. tridentata*.

The characters used in this study were subjected to multivariate analysis, detailed results of which will be published separately. Discriminant functions were derived to maximize separation between groups using principal components (combinations of characters). The first component (67.7% of variance) separated *L. macrostoma* from *L. tridentata*. Disc length exhibited the strongest loading on the first component. The second component (31% of variance) appeared to differentiate among *L. tridentata* at different life stages. This second component was strongly influenced by the morphological changes females undergo prior to spawning.

Lampetra macrostoma differs physiologically from *L. tridentata*. Postlarval *L. macrostoma* survived in freshwater while all attempts to maintain *L. tridentata* were unsuccessful. As *L. tridentata* from the same locations survived in full-strength seawater, it appeared that *L. tridentata* could survive only temporarily in freshwater after metamorphosis was completed, and after feeding commenced in mid-October. Admittedly the failure to maintain *L. tridentata* in freshwater is an inconclusive experiment because the cause of death was not determined. However, the survival of the non-anadromous species under similar conditions and the survival

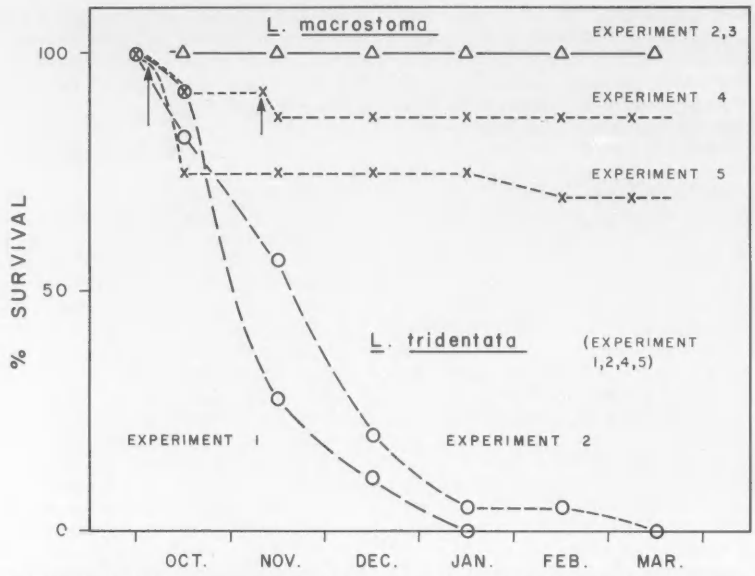

FIG. 4. Survival of *L. macrostoma* and *L. tridentata* in freshwater and *L. tridentata* in salt water. Experiment 1 contained *L. tridentata*, experiment 2 contained *L. tridentata* and *L. macrostoma*, experiment 3 contained *L. macrostoma*, experiment 4 contained *L. tridentata* that were converted from freshwater to salt water in mid-November (position of arrow), and experiment 5 contained *L. tridentata* that were converted to salt water in mid-October (position of arrow).

of *L. tridentata* in seawater strongly suggest that recently metamorphosed *L. tridentata* and *L. macrostoma* differ in their ability to survive in freshwater. It is possible that *L. tridentata* must go to sea while *L. macrostoma* prefers freshwater.

Interestingly, it is not known if the anadromous form of the sea lamprey (*Petromyzon marinus*) can survive in freshwater. It is not an uncommon belief that "landlocked" or non-anadromous forms of the sea lamprey and the Pacific lamprey developed when anadromous forms remained in freshwater and became non-anadromous. Certainly this is one of the theories for explaining the increase in abundance of the sea lamprey in the Great Lakes, yet to my knowledge no one has demonstrated that this is possible within the period being considered. It is possible that the ability to remain in freshwater evolved in the same manner as other specific characteristics (e.g. nonparasitic habits), and that the non-anadromous genotype is not present in the anadromous population.

Lampetra macrostoma as well as the anadromous *L. tridentata* are found in the Lake Cowichan system (Carl 1953). In order that the two species remain distinct, conventional theory would require that some barrier must be present to prevent interbreeding. One possibility is that the spawning of *L. tridentata* occurs earlier than *L. macrostoma* and *L. tridentata* may spawn exclusively in streams while *L. macrostoma* spawn in lakes. Unfortunately, at present there is not enough information to decide if either of these possibilities is valid.

I feel that the morphological and physiological differences are sufficiently distinct and constant to describe this form as a new species. Certainly they are as distinctive as characters currently used to separate other species. However, morphological characters are variable and it is always possible that the specimens examined in this study represent the extremes in the range. While one such study of variations of *L. tridentata* over their geographical range in Oregon concluded that these characters were useful in distinguishing *L. tridentata* from its congeners if fish of similar life history stages were compared (Kan 1975), it is still possible that differences may be found over a broad range. Until more information becomes available to prove or disprove this possibility, I suggest that the new species designation be retained to emphasize the existence of this form and its profound deleterious effect on freshwater fishes, particularly salmonids. When more information becomes available we may conclude that *L. similis*, *L. minima*, and *L. macrostoma* are all subspecies of *L. tridentata*, but until such proof has been produced, I believe it is important to recognize the existence of these distinct forms with a distinct species designation.

Acknowledgments

Much of the information used in this study was collected by a group of volunteers, who used their spare time to study the biology of this new species. I greatly appreciate the interest and enthusiasm of Sue Farlinger, Wendy-Lou Mitton, Heidi Zeis, Mike Smith, Ed Pawlik, Barry Pawlik, John Richards, and Jim Thompson. Other colleagues at the Pacific Biological Station and numerous local residents assisted

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Inshore–Offshore Sedimentation Differences Resulting from Resuspension in the Eastern Basin of Lake Erie[1]

J. BLOESCH

Eidg. Anstalt für Wasserversorgung, Abwasserreinigung und Gewässerschutz (EAWAG), CH-8600 Dübendorf, Switzerland

BLOESCH, J. 1982. Inshore–offshore sedimentation differences resulting from resuspension in the Eastern Basin of Lake Erie. Can. J. Fish. Aquat. Sci. 39: 748–759.

From June through October 1978 sediment traps were moored at three stations in an inshore–offshore transect in the Eastern Basin of Lake Erie. Settling fluxes measured with the traps exposed close to lake bottom were rather similar at all three stations during summer stratification, averaging 6.1 $g \cdot m^{-2} \cdot d^{-1}$ for dry weight, 293 $mg \cdot m^{-2} \cdot d^{-1}$ for particulate organic carbon (POC), 38 $mg \cdot m^{-2} \cdot d^{-1}$ for particulate nitrogen (PN), and 5.44 $mg \cdot m^{-2} \cdot d^{-1}$ for particulate phosphorus (PP). A comparison of the hypolimnetic traps with the epilimnetic traps at the offshore station indicated that considerable resuspension takes place even in summer. During fall, however, the nearshore sedimentation rates were markedly increased because of storm-induced bottom resuspension. By comparing the trap catches with sediment cores taken at all three stations, a resuspension model for dry weight, POC, and PN was developed. The calculations showed that newly formed organic material is resuspended and redeposited more frequently at nearshore locations than offshore. This repeated nearshore resuspension enhances decomposition of detritus, as shown by low relative phytoplankton activity in the hypolimnetic traps, and results in horizontal transport of fine-grained organic matter in the offshore direction. The significant POC and PN concentration differences found in the inshore–offshore transect of the bottom sediments can be explained by these two processes.

Key words: sedimentation, sediment traps, sediment cores, resuspension, inshore–offshore differences

BLOESCH, J. 1982. Inshore–offshore sedimentation differences resulting from resuspension in the Eastern Basin of Lake Erie. Can. J. Fish. Aquat. Sci. 39: 748–759.

De juin à octobre 1978, des trappes à sédiment ont été ancrées à trois stations sur une section allant du rivage vers le large dans le bassin est du lac Érié. Les flux de sédimentation, mesurés avec les trappes exposées près du fond du lac, sont plutôt identiques aux trois stations au moment de la stratification estivale, en moyenne 6,1 $g \cdot m^{-2} \cdot d^{-1}$ pour le poids sec, 293 $mg \cdot m^{-2} \cdot d^{-1}$ pour le carbone organique particulaire (POC), 38 $mg \cdot m^{-2} \cdot d^{-1}$ pour l'azote particulaire (PN) et 5,44 $mg \cdot m^{-2} \cdot d^{-1}$ pour le phosphore particulaire (PP). À la station du large, une comparaison des trappes hypolimnétiques et épilimnétiques démontre que, même en été, il y a resuspension considérable. En automne, cependant, les taux de sédimentation près du rivage augmentent de façon marquée par suite d'une resuspension au fond provoquée par les tempêtes. Nous avons construit un modèle de resuspension pour le poids sec, le POC et le PN en comparant les prises des trappes avec des carottes de sédiment prélevées aux trois stations. Les calculs indiquent que le matériel organique nouvellement formé est resuspendu et redéposé plus fréquemment près du rivage qu'au large. Cette resuspension répétée près du rivage favorise la décomposition des détritus, comme le démontre une activité relativement faible du phytoplancton dans les trappes hypolimnétiques, et résulte en un transport horizontal de fines matières organiques en direction du large. Les différences significatives de POC et de PN dans les sédiments benthiques le long de la section du rivage vers le large peuvent s'expliquer par ces deux processus.

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USUALLY lake models and lake budget calculations are derived from physical, chemical, and biological data collected from a single sampling site (e.g. deepest) or from a few sites strategically located.

Though it is well recognized that overall differences within a lake are present, they are either considered to be negligible, or in most cases too time-consuming and costly to investigate. However, lake-wide surveys have been realized in many Great Lake's studies as a result of the extensive variability associated with these large bodies of water (e.g. Callender 1969; Burns 1976a; Munawar 1978; Kwiatkowski 1978, 1980). In addition, some small lakes have been investigated regarding the problems of horizontal differentiation (Davis 1968, 1973; Davis and Brubaker 1973; Serruya 1977; von Orelli 1980; Evans and Rigler 1980).

Horizontal variabilities in lakes are usually found in different lake basins; however, they may also be present in inshore–offshore transects. These differences between pelagic and littoral locations are dependent on lake size and morphometry. In Lake Erie, inshore–offshore differences have been reported for nutrients (Burns 1976b), phytoplankton standing crop and species composition (Munawar and Munawar 1976), and zooplankton distribution (Watson 1976). Moreover, the texture of surficial sediments shows distinct inshore–offshore differences mainly in the East and Central Basins (Thomas et al. 1976).

The objective of this study was to examine inshore–offshore differences in sedimentation processes in the Eastern Basin of Lake Erie. A hypothesis was formulated that assumed different lake depths, i.e. different sinking distances would influence the mineralization of plankton biomass and detritus. In addition, lake depth would affect settling fluxes caused by sediment resuspension resulting from water turbulence. Thus, the formation of bottom sediments is a dynamic process essentially governed by lake depth and wind-induced currents (Håkanson 1981). It is of crucial importance for whole lake metabolism in which way the sediments are affected by sedimentation, resuspension, transport and redeposition, release, and final burial of particulate carbon, nitrogen, and phosphorus. One possible method to quantify these processes is the combined analysis of settling particulate matter (sediment traps) and bottom deposits (cores) (Bloesch 1977).

Methods

From June 28 through October 10, 1978, cylindrical sediment traps (height 91.4 cm, diameter 6.6 cm, see fig. 8 in Bloesch and Burns 1980) were exposed at three stations (Fig. 1) and retrieved at biweekly intervals. Experiments conducted on trap efficiency proved the validity of these traps and the exposure time (see tables 2, 5–7 in Bloesch and Burns 1980). No resuspension of settled material within the traps was observed upon retrieval, thus the supernatant water was drained off and the sediment samples were taken from the last litre of each of the five replicate traps.

Dry weight was measured gravimetrically by centrifuging homogeneously mixed subsamples (400–800 mL) and drying at 50°C for a minimum of 48 h. Chemical analysis of particulate matter was carried out on material that had been dried on filters. Subsamples (10–100 mL) were filtered through Whatman GF/C glass fiber filters, preheated at

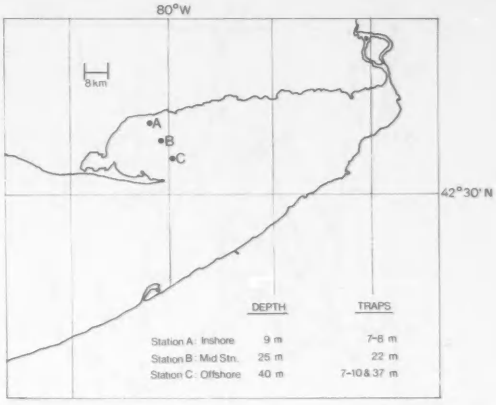


FIG. 1. Eastern Basin of Lake Erie. Sampling and trap mooring sites (A, B, C).

500°C, for particulate organic carbon (POC), particulate nitrogen (PN), and chlorophyll (chl *a*) analysis, and through Millipore HA 0.45-μm filters for particulate phosphorus (PP) analysis, respectively. POC and PN were analyzed with a Hewlett Packard 185 CHN analyzer after filter treatment with acidified water (0.3 mL H_2SO_4/100 mL H_2O) to remove inorganic C, and PP was analyzed colorimetrically with a Technicon AA II autoanalyzer (ammonium molybdate, $SnCl_2$, 660 nm) after digesting the filters in 50 mL acidified water (1 mL 30% H_2SO_4/100 mL H_2O). Chl *a* was measured and corrected for pheo-pigments according to Strickland and Parsons (1972). Biological subsamples were counted for phytoplankton with an inverted microscope (Utermöhl 1958), and ^{14}C-experiments (liquid scintillation technique, Vollenweider 1974) were used to measure primary productivity and relative activity of phytoplankton in the traps. One hundred and fifteen-millilitre bottles were usually exposed for 5 h during trap exchange between 09:00 and 16:00 in the depth of 1 and 5 m for water samples, and in the depth of trap position for the trap samples. After retrieval, 25 mL were filtered through Sartorius cellulose nitrate filters (0.45 μm, No. 11306), acidified with 0.5 mL 0.5 N HCl, and dissolved with 10 mL PCS scintillator.

At the beginning of October, sediment cores were taken at all three stations with a gravity corer. The cores were sectioned into ½-cm slices from 0 to 3 cm and into 1-cm slices from 3 to 5 cm (stations B and C), and into 1-cm slices from 0 to 5 cm (station A), respectively. After drying at 50°C, these subsamples were pulverized and analyzed for POC, PN, and PP with the same methods as the trap material.

In an accompanying program, the lake was investigated also in the inshore–offshore transect, and water temperature was measured in situ by EBT (electronic bathythermograph) profiles. Chemical water analysis included P, N, and C components: soluble reactive phosphorus (SRP) was measured colorimetrically at 660 nm in an autoanalyzer using ammonium molybdate and $SnCl_2$ as reagents. Total phosphorus was analyzed as for SRP after digestion with H_2SO_4 (1 mL 30% H_2SO_4/100 mL H_2O) and $K_2S_2O_8$ in an autoclave for 30 min at about 112°C. PP was calculated by subtracting total

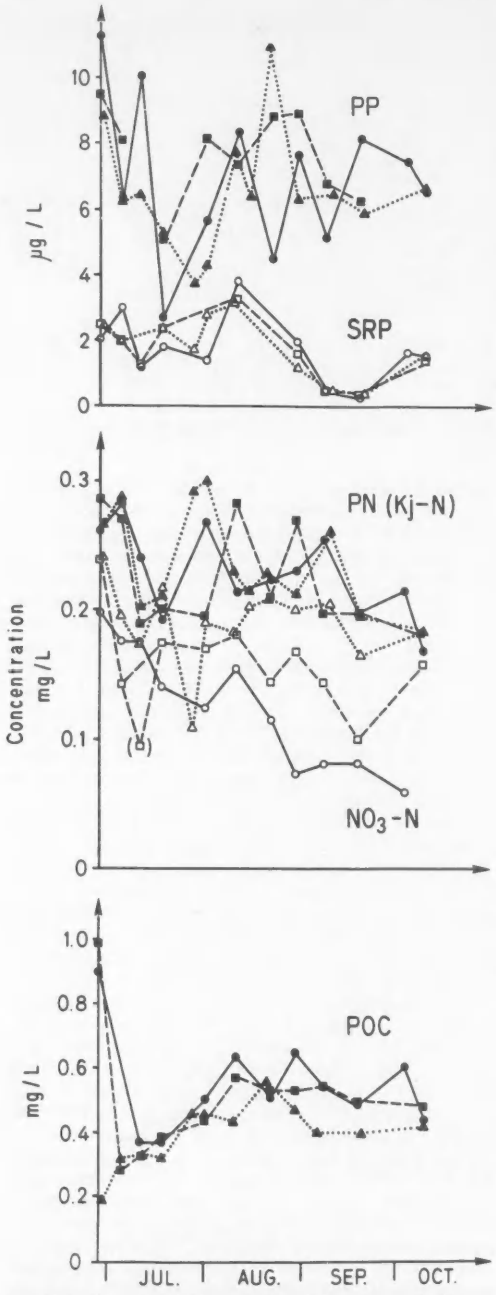


FIG. 2. P, N, and C inshore–offshore differences in the Eastern Basin of Lake Erie, June–October 1978. Mean concentrations in total water mass: ●, ○ inshore station A; ■, □ mid-station B; ▲, △ offshore station C.

P in the filtrate from total P in the unfiltered samples, while nitrate plus nitrite were measured colorimetrically at 550 nm in an autoanalyzer with cadmium reduction and sulfanylamide/naphtylendiamine as reagents. PN (total Kjeldahl nitrogen) was measured with the method of El-Kei (1976), and POC was analyzed with a Hewlett Packard 185 CHN analyzer in the same way as sediment samples.

Results

The results are presented in the sequence of (1) lake water, where particulate matter is produced and suspended; (2) sediment traps to follow the sinking process of particles; and (3) bottom sediments, where the settling particles are deposited.

1) The P, N, and C components in the water vary seasonally for each of the three sampling locations on the inshore–offshore transect (Fig. 2). A nutrient depletion caused by phytoplanktonic activity is evident for both SRP and NO_3, while the fluctuations of the particulates were rather irregular. The inshore–offshore difference in SRP was very slight whereas NO_3 showed a large change in concentration increasing from station A nearshore to station C offshore. Of the particulate variables, PP showed the greatest inshore–offshore difference while PN indicated only slight differences, and POC showed the least change horizontally.

Temperature profiles (isotherms in Fig. 3) indicate sharp differences in the horizontal transect. Offshore station C was stratified during the entire study period, whereas the nearshore station A was not found to be normally stratified during summer. At this station A the water column was sometimes isothermal from surface to bottom, but the isothermal conditions were periodically interrupted by inflowing cold-water masses from the deeper portions of the lake (arrows in Fig. 3). Though mid-station B also showed indications of these cold-water movements, this station was similar to the offshore station C in the stability of the thermal structure. The nearshore station was the first site with an entire circulation, when the water temperature started to decrease gradually in the early fall. By late September, fall turnover was all but complete at the mid-station B, while the offshore station was still stratified at the end of the study period on October 10.

The biological variables primary production, phytoplankton biomass, and chlorophyll *a* (Fig. 4 and 5) did not show great inshore–offshore differences. The phytoplankton developed peak biomass at offshore station C in September, but chl *a* concentrations were greatest at nearshore station A during the same period. Detailed phytoplankton results were obtained during this study by M. Munawar and D. B. Shindler (unpublished data).

2) During the summer months (June 28 through September 8) when the water was stratified, settling fluxes measured near bottom were similar at all three stations, averaging 6.1 $g \cdot m^{-2} \cdot d^{-1}$ for dry weight, 293 $mg \cdot m^{-2} \cdot d^{-1}$ for POC, 38 $mg \cdot m^{-2} \cdot d^{-1}$ for PN, and 5.44 $mg \cdot m^{-2} \cdot d^{-1}$ for PP (Table 1). When fall turnover was initiated in early September by decreasing temperatures and increasing storm activity, trap catches increased 6–13 times at the nearshore station (depth 9 m). This apparent change in sedimentation must have been the result of resuspension of bottom sediments. Because no stratification of the water column existed in this location, storm-induced turbulence reached the sediment–

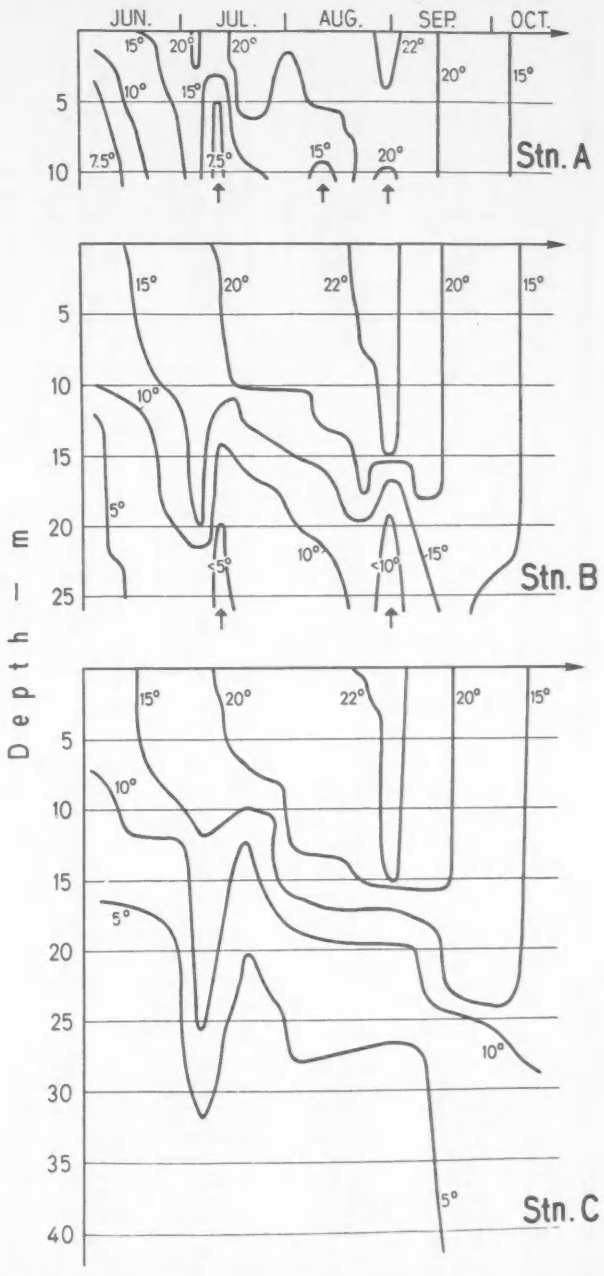
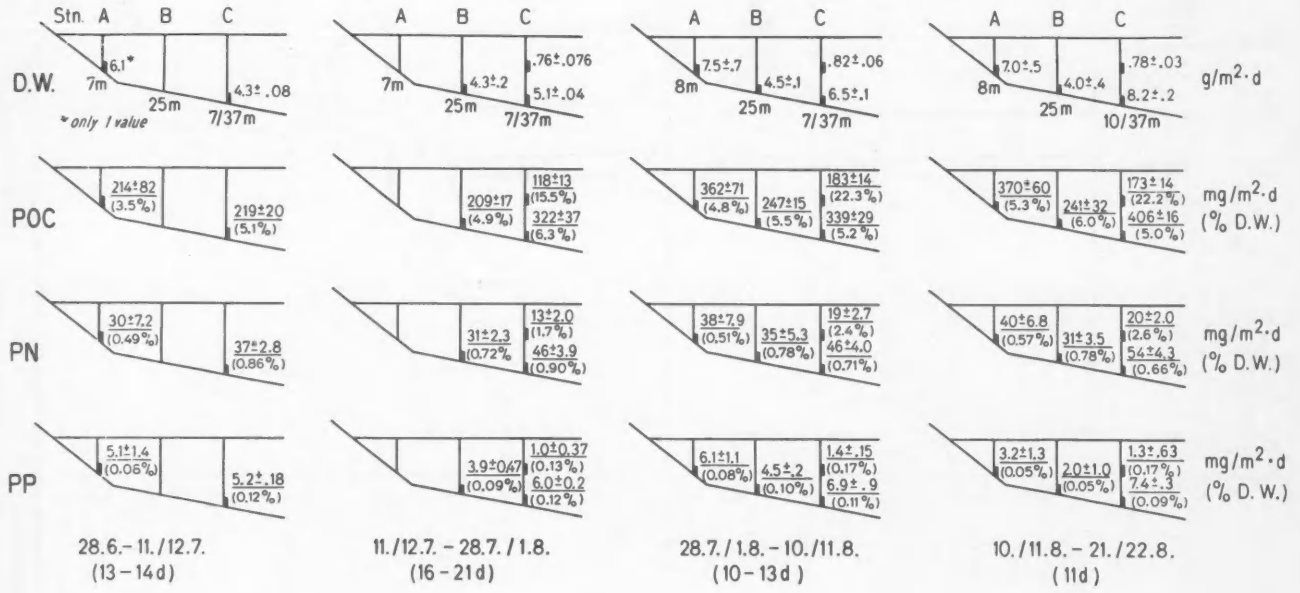
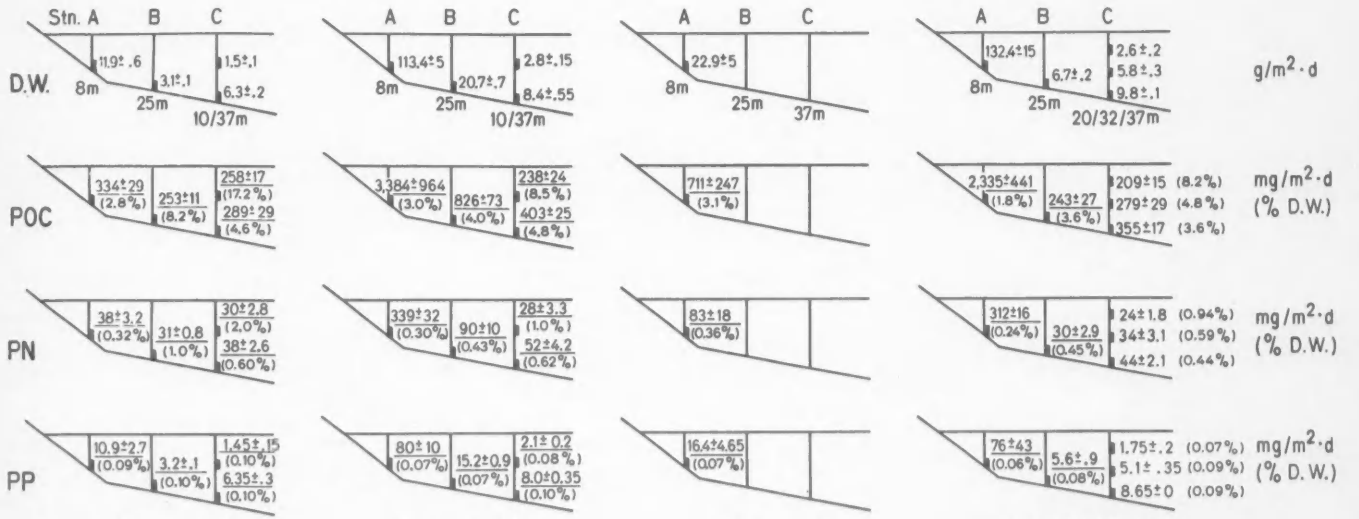


FIG. 3. Temperature inshore–offshore differences in the Eastern Basin of Lake Erie, June–October 1978. Isotherms (°C).

TABLE 1. Inshore–offshore differences in dry weight (D.W.), POC, PN, and PP sedimentation in the Eastern Basin of Lake Erie, June 28–Oct. 10, 1978. Mean values of five replicates, g and $mg \cdot m^{-2} \cdot d^{-1}$, values in parentheses as percent dry weight.




Stn. A B C
D.W.
11.9±.6
8m
3.1±.1
25m
1.5±.1
6.3±.2
10/37m
g/m2·d
A B C
113.4±5
20.7±.7
2.8±.15
8.4±.55
10/37m
A B C
22.9±5
25m
37m
A B C
132.4±15
6.7±.2
2.6±.2
5.8±.3
9.8±.1
20/32/37m
POC
334±29 (2.8%)
253±11 (8.2%)
258±17 (17.2%)
289±29 (4.6%)
3,384±964 (3.0%)
826±73 (4.0%)
238±24 (8.5%)
403±25 (4.8%)
711±247 (3.1%)
2,335±441 (1.8%)
243±27 (3.6%)
209±15 (8.2%)
279±29 (4.8%)
355±17 (3.6%)
mg/m2·d
(% D.W.)
PN
38±3.2 (0.32%)
31±0.8 (1.0%)
30±2.8 (2.0%)
38±2.6 (0.60%)
339±32 (0.30%)
90±10 (0.43%)
28±3.3 (1.0%)
52±4.2 (0.62%)
83±18 (0.36%)
312±16 (0.24%)
30±2.9 (0.45%)
24±1.8 (0.94%)
34±3.1 (0.59%)
44±2.1 (0.44%)
mg/m2·d
(% D.W.)
PP
10.9±2.7 (0.09%)
3.2±.1 (0.10%)
1.45±.15 (0.10%)
6.35±.3 (0.10%)
80±10 (0.07%)
15.2±0.9 (0.07%)
2.1±0.2 (0.08%)
8.0±0.35 (0.10%)
16.4±4.65 (0.07%)
76±43 (0.06%)
5.6±.9 (0.08%)
1.75±.2 (0.07%)
5.1±.35 (0.09%)
8.65±0 (0.09%)
mg/m2·d
(% D.W.)
21./22.8.–6./8.9.
(16–17d)
6./8.9.–19./20.9.
(11–14d)
19.9.–4.10.
(15d)
19./20.9. [4.10.]–10.10.
(20–21 [6] d)

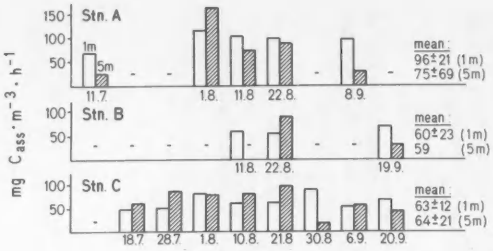


FIG. 4. Inshore–offshore differences in primary production in the Eastern Basin of Lake Erie, July–September 1978.

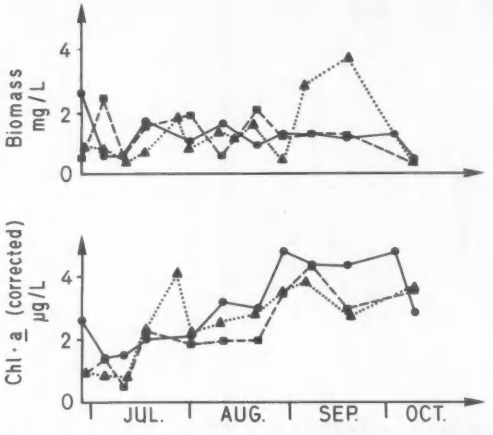


FIG. 5. Phytoplankton biomass and chlorophyll *a* (corrected) inshore–offshore differences in the Eastern Basin of Lake Erie, June–October 1978. Mean concentrations in the epilimnion: ●, inshore station A; ■, mid-station B; ▲, offshore station C.

water interface and subsequently mixed the sediments into the overlying water which then settled into the traps. During the same period, weaker mixing of the bottom sediments at the mid-station (depth 25 m) was evident by a flux increase of 1.5–2.5. The thin hypolimnion remaining at this station provided enough insulation from the storm-induced turbulence to shield sufficiently the sediment–water interface to prevent the mixing that occurs in the unstratified areas. At the offshore location (depth 40 m) where the hypolimnion was still over 10 m thick, sedimentation rates were only slightly greater than those measured during the summer months. The effect of resuspension was diminished during the second half of September at station A nearshore as a result of calm weather conditions, but again increased at the beginning of October when storms intensified.

At the offshore station settling fluxes were also measured in the epilimnion just above the thermocline (trap depth 7/10/20 m; the traps were lowered three times during the study period according to the downward movement of the metalimnion). The average sedimentation rates in summer were 1 $g \cdot m^{-2} \cdot d^{-1}$ for dry weight, 183 $mg \cdot m^{-2} \cdot d^{-1}$ for POC, 20.5 $mg \cdot m^{-2} \cdot d^{-1}$ for PN, and 1.3 $mg \cdot m^{-2} \cdot d^{-1}$ for PP. These rates were markedly smaller than those measured in the hypolimnetic traps during the same period. Epilimnetic settling fluxes for POC and PN were 1.2–3 times less, and the dry weight and PP were 4–20 times less than the fluxes measured in the hypolimnion. Resuspension of bottom sediments into the hypolimnion was considered responsible for these differences in sedimentation rates. However, the composition of the sedimentary material differed in the two both the hypo- and epi-limnion. For example, POC and PN (as percent dry weight) were less in the hypolimnion than in the epilimnion. The PP %, however, was almost the same. These differences mean that the resuspended sediment at station C consists of material with relatively low organic content.

The phytoplankton settling fluxes during summer (Table 2) averaged 586 mg biomass $\cdot m^{-2} \cdot d^{-1}$ in the epilimnetic traps at offshore station C and 243 mg biomass $\cdot m^{-2} \cdot d^{-1}$ in the hypolimnetic traps of all three stations. There was no distinct inshore–offshore variation. However, during the fall, resuspension was evident at nearshore station A where the fluxes were increased 3–5 times.

By means of autoradiography it is possible to estimate the portion of live and dead cells of the entrapped algal species. In our samples (M. Munawar and D. B. Shindler unpublished data) the flagellates were the most active phytoplankters; however, they were not abundant in the traps, as they are rapidly decomposed during settling as a result of their delicate cell walls. The dominant greens and diatoms were usually senescent or dead, especially in the deeper traps. The total phytoplankton community in the hypolimnetic traps of stations B and C was mostly inactive (Table 3), whereas the phytoplankton activity increased 5–10 times in the bottom trap of nearshore station A. The highest activity, however, was found in the epilimnetic trap at offshore station C. These findings suggest that most of the activity of algae is lost after a settling distance of about 25 m.

The settling fluxes of chlorophyll *a* in summer averaged 1240, 650, and 1160 $\mu g \cdot m^{-2} \cdot d^{-1}$ in the hypolimnetic traps at stations A, B, and C, respectively, and were relatively low in the epilimnetic traps at offshore station C when compared with the phytoplankton biomass (mean value for summer stratification 900 $\mu g \cdot m^{-2} \cdot d^{-1}$, Table 4).

3) The composition of sediment which could be resuspended was obtained from cores taken at each of the three stations at the beginning of October and analyzed for POC, PN, and PP content (Table 5). These components were distributed quite homogeneously in the upper 3–5 cm of the sediments. Significant inshore–offshore differences show an increasing concentration gradient from station A to station C. These differences can be explained by the similar distribution of the clay-size fraction in the sediment according to Thomas et al. (1976), who interpreted the inshore-to-offshore decrease in grain size to reflect decreasing energy with increasing water depth. This general statement is illustrated by the temperature profiles at the beginning of October 1978, when inshore and mid-lake stations were circulating to the lake bottom, and the offshore station was still stratified (Fig. 3).

TABLE 2. Inshore–offshore differences in phytoplankton biomass sedimentation in the Eastern Basin of Lake Erie, July 11–Oct. 10, 1978 ($mg \cdot m^{-2} \cdot d^{-1}$).

Date (1978)	Exposure time, d	Station A 7/8 m[a]	Station B 25 m	Station C 7/10/20 m[a]	Station C 37 m
July 11–12	13/14	91	—	—	272
July 18	6	—	—	—	194
July 28	16	—	—	652	224
Aug. 1	21/4	—	177	—	214
Aug. 10–11	10/13	253	195	765	590
Aug. 15	5	—	—	—	425
Aug. 21–22	11	287	144	252	159
Aug. 30	9	—	—	—	174
Sept. 6–8	17/16	347	191	676	196
Sept. 19–20	11/14	1288	340	164 ?	401
Oct. 4	15	166	—	—	—
Oct. 10	6/21/20	1348	142	202	233

[a]The traps were lowered three times during the study period according to the downward movement of the metalimnion.

TABLE 3. Relative activity of phytoplankton in the traps exposed in the inshore–offshore transect in the Eastern Basin of Lake Erie, August–September 1978. Primary production: $\mu g\ C_{ass} \cdot trap\ area^{-1} \cdot h^{-1}$ (mean of duplicates); trap area = 34.25 cm^2.

Date (1978)	Station A 8 m	Station B 25 m	Station C 7/10 m[a]	Station C 37 m
Aug. 10–11	284	20	2820	34
Aug. 21–22	413	46	707	47
Aug. 30	—	—	—	35
Sept. 6–8	168	—	393	17
Sept. 19–20	—	52	390	163
Mean	288	39	1078	59

[a]The traps were lowered three times during the study period according to the downward movement of the metalimnion.

Resuspension Model

Comparison of the core and trap results (Table 5 vs. Table 1) shows that PP concentrations of the bottom sediments are slightly higher than PP concentrations in trapped material at all three stations. In contrast, POC and PN contents were higher in the traps by a factor of 5–6 at the inshore station, by a factor of 4 at station B, and 0.5 times greater at the offshore station. These differences are the basis for the resuspension model presented.

The amount as well as the origin of the entrapped resuspended material can be estimated by the following calculations and statements illustrated in Fig. 6. Total resuspension fluxes R_D, R_C, R_N, R_P at offshore station C during summer stratification are calculated by equation (1):

$$(1)\quad R_D = T_D - E_D;\quad R_C = T_C - E_C;\quad \text{etc.},$$

assuming epilimnion traps represent the net downward flux near lake bottom, while the bottom traps represent the net downward flux plus resuspension. The results in Table 6 show a surprisingly high resuspension, contributing about 50% of the POC and PN and about 80% of the PP and dry weight material to the trap catches. Even if we would assume possible mineralization at a rate of 40% in the epilimnetic traps (Rathke et al. 1981), decreasing the calculated values, resus-

TABLE 4. Inshore–offshore differences in chlorophyll *a* (corrected) sedimentation in the Eastern Basin of Lake Erie, July 11–Oct. 10, 1978. ($\mu g \cdot m^{-2} \cdot d^{-1}$, mean values of five replicates.)

Date (1978)	Exposure time, d	Station A 7/8 m[a]	Station B 25 m	Station C 7/10/20 m[a]	Station C 37 m
July 11–12	13/14	321	—	—	907
July 18	6	—	—	—	1805
July 28	16	—	—	574	1682
Aug. 1	21/4	—	623	—	946
Aug. 10–11	10/13	871	536	635	1168
Aug. 21–22	11	1106	405	799	806
Aug. 30	9	—	—	—	833
Sept. 6–8	17/16	2658	1048	1584	1120
Sept. 19–20	11/14	6560	2326	1024	1896
Oct. 4	15	2446	—	—	—
Oct. 10	6/21/20	5105	644	1277	1729

[a]The traps were lowered three times during the study period according to the downward movement of the metalimnion.

TABLE 5. Inshore–offshore differences in bottom sediments of Eastern Lake Erie. Cores taken on Oct. 4, 1978, at the inshore and mid-stations, on Oct. 10, 1978, at the offshore station. Mean values from the upper 3 cm of the cores in % of dry weight.

	Station A inshore	Station B midshore	Station C offshore
POC	0.31	0.62	2.13
PN	0.04	0.10	0.32
PP	0.076	0.085	0.120

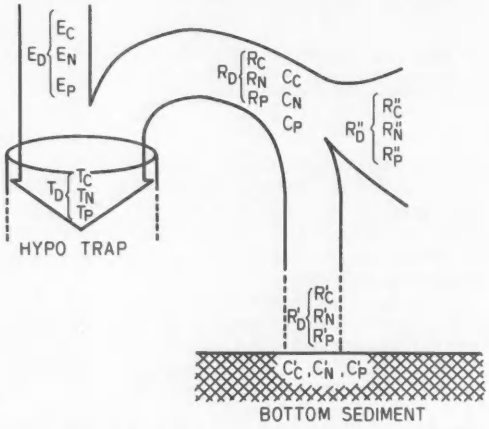


FIG. 6. Catch of a sediment trap exposed near lake bottom, general model used for calculations of resuspension.
E_D, E_C, E_N, E_P represents measured total dry weight, POC, PN, and PP flux in epi-traps;
T_D, T_C, T_N, T_P represents measured total dry weight, POC, PN, and PP flux in hypo-traps;
R_D, R_C, R_N, R_P represents measured total dry weight, POC, PN, and PP flux in hypo-traps due to resuspension;
$C_C = \frac{R_C}{R_D}$, $C_N = \frac{R_N}{R_D}$, $C_P = \frac{R_P}{R_D}$ represents concentration of POC, PN, and PP in dry weight material resuspended into the hypo-traps;
R'_D, R'_C, R'_N, R'_P represents total dry weight, POC, PN, and PP resuspension flux consisting of bottom sediments originating from the vicinity of the traps;
$C'_C = \frac{R'_C}{R'_D}$, $C'_N = \frac{R'_N}{R'_D}$, $C'_P = \frac{R'_P}{R'_D}$ represents measured concentration of POC, PN, and PP in dry weight material from bottom sediments in the vicinity of the traps;
R''_D, R''_C, R''_N, R''_P represents total dry weight, POC, PN, and PP resuspension flux consisting of material with other composition than the bottom sediments in the vicinity of the traps.

pension would still amount to 83% for dry weight, 10% for POC, 26% for PN, and 68% for PP, respectively. On the other hand, mineralization processes are also effective in the hypolimnetic traps (causing a loss of material in the order of 10% (Bloesch and Burns 1980)) and during sedimentation in the hypolimnion, thus increasing the minimum amount of resuspension presented in Table 6 to an unknown degree.

Fall resuspension for all three stations is calculated in the same manner, using the mean of the four summer values from the epilimnetic traps at station C as the general net downward flux over the inshore–offshore transect, and the trap catches of September 19 as representative of both downward flux and resuspension (Table 7). At offshore station C the calculation shows only a slight increase over the summer resuspension estimates, as would be expected because this station was still stratified. In contrast the two nearshore stations showed a considerably increased resuspension rate, particularly at station A.

Resuspension in the fall cannot consist totally of material from bottom sediments originating in the vicinity of the station, because the POC, PN, and PP concentration of the trapped resuspended material (Table 8) is not the same as the measured concentration found in the cores (Table 5). The trap POC and PN contents are greater than found for the cores; this difference decreases from inshore to offshore. The trapped PP

TABLE 6. Resuspension (in % of bottom trap catch) during summer stratification. Offshore station C, Eastern Basin of Lake Erie 1978.

Date (1978)	Dry wt, %	POC, %	PN, %	PP, %
July 12–28	85	63	71	83
July 28–Aug. 10	87	46	59	80
Aug. 10–21	90	57	63	82
Aug. 21–Sept. 6	76	11	21	77
Mean	85	46	55	81
Mean, corrected	83	10	26	68

TABLE 7. Inshore–offshore differences in resuspension (in % of bottom trap catch) during fall. Eastern Basin of Lake Erie, Sept. 19, 1978.

	Dry wt, %	POC, %	PN, %	PP, %
Station A	99	95	94	98
Station B	95	78	77	92
Station C	88	55	61	84

TABLE 8. Total fall resuspension flux measured by the hypolimnetic traps, and composition of resuspended dry weight material.

Station	Component	Flux $mg \cdot m^{-2} \cdot d^{-1}$	Concn. % of dry wt
A	Dry wt	112 430	—
	POC	3 201	2.85
	PN	318.5	0.28
	PP	78.7	0.070
B	Dry wt	19 730	—
	POC	643	3.26
	PN	69.5	0.35
	PP	13.9	0.071
C	Dry wt	7 430	—
	POC	220	2.96
	PN	31.5	0.42
	PP	6.7	0.090

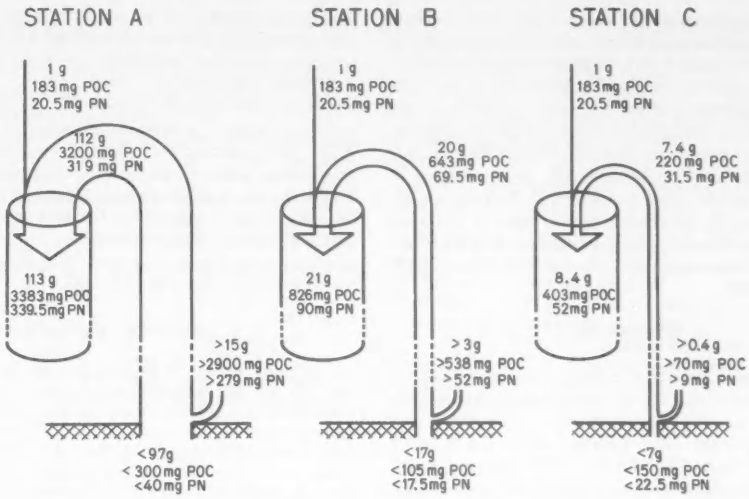


FIG. 7. Models of calculated dry weight, POC, and PN resuspension at the inshore and offshore stations in the Eastern Basin of Lake Erie, Sept. 19, 1978. Values in g or $mg \cdot m^{-2} \cdot d^{-1}$.

content is not significantly different from that found for the cores at all three stations. Consequently

$$R'_D < R_D,$$

$$R'_C = C'_C \cdot R'_D < C_C \cdot R_D = R_C,$$

$$R'_N = C'_N \cdot R'_D < C_N \cdot R_D = R_N,$$

$$\text{and } R'_P = C'_P \cdot R'_D \simeq C_P \cdot R_D = R_P.$$

The maximum dry weight flux from the bottom sediments in the vicinity of the traps, R'_D, can be calculated according to equation (2) by using the POC and PN concentrations of trap and core material (this calculation is not valid for PP because of the insignificant differences between R_P/R_D and R'_P/R'_D):

$$(2) \quad \frac{R_C}{R_D} = x \cdot \frac{R'_C}{R'_D} + (1 - x) \cdot \frac{R''_C}{R''_D}$$

$$\text{and } \frac{R_N}{R_D} = x \cdot \frac{R'_N}{R'_D} + (1 - x) \cdot \frac{R''_N}{R''_D}$$

where x = portion of dry weight resuspension flux from bottom sediments originating in the vicinity of the station, $1 - x$ = portion of dry weight resuspension flux consisting of material with other composition than the bottom sediments in the vicinity of the traps,

$$\text{and } \frac{R''_C}{R''_D} \leqq \frac{E_C}{E_D}; \quad \frac{R''_N}{R''_D} \leqq \frac{E_N}{E_D}$$

assuming that the material originating from other than bottom sediments has maximum possible POC and PN concentrations similar to that in the material caught in the epilimnetic traps. It is evident that the remaining minimum flux of resuspended material originating from other than the vicinity of the station, $R''_D = R_D - R'_D$, must contain more POC and PN than has been found in the sediments at all three stations, but certainly not more than has been found in the epilimnetic traps. Because a horizontal transport of resuspended POC- and PN-rich bottom sediments originating from offshore regions towards the shore seems unlikely, I assume that fresh material sinking down from the epilimnion is resuspended and redeposited repeatedly over an infinite time period. The existence of such a vertical cycle is supported because no distinct accumulation of POC and PN could be detected in the upper 5–10 mm of the cores.

The results of these model calculations, summarized in Fig. 7, show that at the offshore station C a large portion of dry weight resuspension is originating from bottom sediments in the vicinity of the station (R'_D), whereas only a small fraction represents fresh material originating from the epilimnion (R''_D). The ratios between the corresponding POC and PN fluxes (R'_C vs. R''_C and R'_N vs. R''_N) are distinctly smaller, because POC and PN concentrations are much higher in the freshly sedimenting material.

At the nearshore stations A and B these ratios are decreased significantly. Because R''_D is 38 times greater at station A than at station C, whereas this factor is only 14 when comparing R'_D, it is obvious that this vertical cycle is much more intensive at nearshore locations than in offshore regions. Consequently, the frequently resuspended organic material sinking down from the epilimnion is decomposed to a greater extent before its final burial at nearshore locations, because conditions for mineralization are more favorable in the water mass than in the sediments.

Phytoplankton is undoubtedly already decomposed to a great extent in the epilimnion, considering the favorable temperatures (>20°C) for mineralization and the relatively low

sinking velocities of algae (<50 cm·d^{-1}, Rathke et al. 1981), enabling a mean epilimnetic (above 10 m) residence time of at least 20 d. The ratio of POC to algal C (taken as 10% of phytoplankton fresh weight (Nauwerck 1963)) indicates that 77% of POC is detrital C in the epilimnetic traps at offshore station C. However, the detrital fraction of POC amounted to 91–95% in the near-bottom traps of all three stations, and most of the trapped phytoplankton cells were senescent or dead (Table 3, and M. Munawar and D. B. Shindler unpublished data). In fall, the resuspended material at station A mainly consisted of detritus because the measured nearshore phytoplankton fluxes increased only 3 times, whereas POC increased 8 times.

Discussion

The phenomenon of bottom resuspension is well known to interfere with measurements of sedimentation rates and has been the subject of many attempts to apply a correction (Davis 1968, 1973; Edwards 1973; Charlton 1975; Gasith 1975; Lastein 1976; Johnson 1977; Serruya 1977). The application of an appropriate correction factor enables the interpretation of settling fluxes measured with traps which have been moored too close to the bottom of deeper lakes, when resuspension is recognized to have caused interferences. However, strong resuspension prevents the use of traps in very shallow and highly turbulent water bodies.

Lake Erie is shallow, having a mean depth of less than 25 m. The Eastern Basin is the deepest segment (max. depth 64 m) with an east–west wind fetch of about 400 km. Consequently the lake is very susceptible to wind-induced turbulence and bottom resuspension. The traps, despite being moored 3 m above the bottom, were still close enough to the bottom that the measurement of net downward settling fluxes were subject to interference by resuspension. A vertical set of traps in the hypolimnion would provide information about the thickness of the water layer that is affected by resuspension.

Neither particulate suspended material (Fig. 2) nor phytoplankton biomass and primary production (Fig. 4 and 5) showed distinct inshore–offshore differences during the study period from June through October 1978. The settling fluxes to the lake bottom measured with traps through the summer months are uniform at all three stations with only small variations. However, the nearshore station changed dramatically in the early fall. The greatly increased sedimentation rates near the lake bottom in the shore zone must result from current- or turbulence-induced resuspension of the sediments. Even in the lower energy zone of station C the differences between fluxes in the epilimnion and hypolimnion indicate a high amount of resuspension taking place during summer (Table 6). Because of the near level bottom of Lake Erie, sediment accumulation in the deeper water zones in and around station C caused by slumping of sediments does not seem to be the explanation for increase in hypolimnion rates, thus resuspension is considered to be the major factor. In Lake Erie sediment focusing is initiated by water currents that redistribute settled material.

The bottom sediments showed significant inshore–offshore differences in POC and PN concentrations (Table 5). These differences cannot be explained by different vertical sedimentation inputs of organic material. The intensive nearshore resuspension, induced mainly in fall by storms, intensifies decomposition of settling organic material and causes a sorting of grain size, with greater particles buried nearshore and finer particles kept suspended in the water and transported in the offshore direction where they can settle to the lake bottom because of a decrease in turbulence (Thomas et al. 1976). Both processes of enhanced mineralization and particle sorting, which are the result of wind-induced turbulence, lead to the low content of organic material in nearshore lake sediments and are responsible for the POC and PN concentration differences found between the cores (Table 5). This emphasizes the crucial importance of nearshore resuspension for overall metabolism of Lake Erie.

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Zooplankton and Micronekton Abundance in Acoustic Scattering Layers on the Nova Scotian Slope

D. D. SAMEOTO

Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

SAMEOTO, D. D. 1982. Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. Can. J. Fish. Aquat. Sci. 39: 760–777.

Zooplankton and micronekton sampling with a multiple net sampler, the BIONESS, in conjunction with a 120-kHz sounder showed significantly higher numbers of animals on the shelf water side of the shelf–slope water front than in the slope water on the Nova Scotian slope. The dominant copepod in the shelf water was *Calanus finmarchicus* and in the slope water it was *Pleuromamma borealis*. The dominant forms of micronekton were the myctophid *Benthosema glaciale* and the euphausiid *Thysanoessa longicaudata*. *Calanus finmarchicus* preferred a temperature of about 6°C, *B. glaciale* a temperature <12°C. The intense acoustic scattering in the shelf water was probably due to the myctophids and euphausiids. The acoustic scattering disappeared once the warmer slope water was entered. The biomass and numbers of each species of zooplankton and micronekton $\cdot m^{-2}$ are given for the shelf and slope water masses, for May 1977 and April 1979; these values are also given for the shelf water in June 1978. Estimates were made of the daily consumption of zooplankton by the euphausiids and myctophids in the two water masses, and it was found that both groups of animals were major consumers of the zooplankton during the spring period. There was no evidence for a food chain dominated by tunicates, chaetognaths, or gelatinous carnivores.

Key words: zooplankton, micronekton, copepod, euphausiid, myctophid, acoustic scattering layer, shelf, slope

SAMEOTO, D. D. 1982. Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. Can. J. Fish. Aquat. Sci. 39: 760–777.

L'échantillonnage du zooplancton et du micronecton à l'aide d'un échantillonneur à filets multiples, le BIONESS, concurremment avec un sondeur de 120 kHz indique la présence d'un nombre nettement supérieur d'animaux sur le côté eau de plateau que du côté eau de pente du front eau de plateau/eau de pente du talus de la Nouvelle-Écosse. Le copépode dominant dans l'eau de plateau est *Calanus finmarchicus* et celui de l'eau de pente est *Pleuromamma borealis*. Les formes dominantes de micronecton sont le myctophide *Benthosema glaciale* et l'euphauside *Thysanoessa longicaudata*. *Calanus finmarchicus* préfère une température d'environ 6°C, *B. glaciale* une température de <12°C. L'intense diffusion acoustique observée dans l'eau de plateau est, je crois, due à la présence de myctophides et d'euphausides. La couche diffusante disparaît au moment de la pénétration dans l'eau de pente, plus chaude. Nous présentons la biomasse et le nombre de chaque espèce de zooplanctontes et de micronectontes $\cdot m^{-2}$ dans les masses d'eau de plateau et de pente en mai 1977 et avril 1979; ainsi que les mêmes valeurs pour l'eau de plateau en juin 1978. La consommation quotidienne de zooplancton par les euphausides et les myctophides des deux masses d'eau a été estimée; les deux groupes d'animaux sont les principaux consommateurs de zooplancton au printemps. Nous n'avons pas de preuve de l'existence d'une chaîne alimentaire dominée par les tuniciers, les chétognathes ou les carnivores gélatineux.

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MILLS and Fournier (1979) compared the Nova Scotian shelf ecosystem with that of the North Sea and stated that although the primary production of the Scotian shelf was 17% higher, the zooplankton production was 31% lower than the North Sea. They also estimated the overall fish production to be 47% lower per unit area in the Nova Scotian system due primarily to a lower pelagic fish catch on the Nova Scotian slope. They accounted for the difference by suggesting that the microzooplankton and gelatinous filter feeding and carnivorous zooplankton were a more important component of the Scotian shelf system than the sample data base indicated. They did not consider the micronekton community, animals between 1 and 10 cm in length, in the analysis. These animals are primarily

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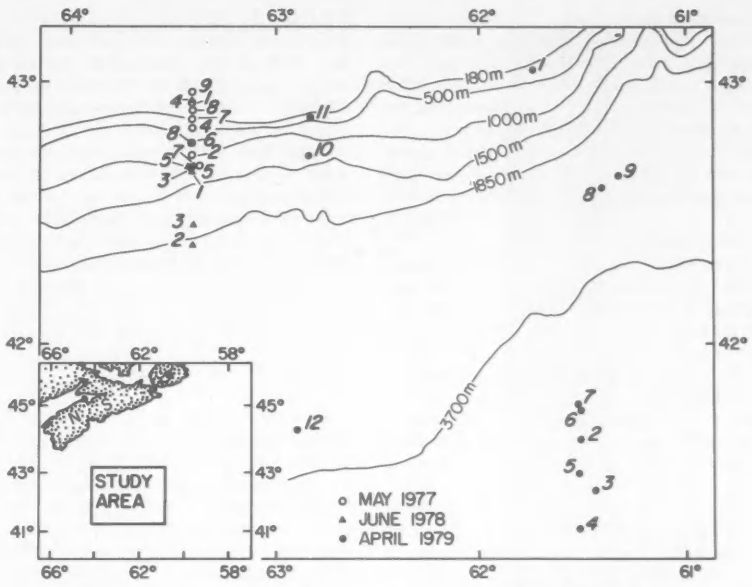


FIG. 1. Station locations for three cruises on the Nova Scotian shelf and slope.

carnivorous, feeding on zooplankton (animals less than 1 cm in length), and form an important link between the zooplankton feeding on the primary producers and the larger pelagic fish which feed on the micronekton.

Halliday (1970) reported that a large population of the myctophid *Benthosema glaciale* was present on the slope of the Nova Scotian shelf. Gjosaeter and Kawaguchi (1980) reported that evidence from acoustic studies along the northeastern Atlantic Coast indicated a stock of myctophids as high as 10 g/m^2. Therefore, it was possible that the lower pelagic commercial fish production reported by Mills and Fournier was due in part to energy being diverted into myctophid production. The main purpose of my study was to determine the importance of myctophids and other micronekton as predators of the zooplankton community on the slope of the Nova Scotian shelf. In addition, I determined the abundance of different species of zooplankton in the shelf and slope waters during the period following the spring bloom.

The study area was between the edge of the Nova Scotian shelf and the region of the shelf–slope water front (Fournier et al. 1977). The physical oceanography and some aspects of the biology of the frontal region located south of the shelf break have recently been described in detail (Fournier et al. 1977; Herman and Denman 1979; Herman et al. 1981). This is a region of high primary productivity during the spring because of vertical mixing of high nutrient slope water with shelf water.

Methods

BIOLOGICAL SAMPLING

The study area extended from the Nova Scotian shelf edge, ~250 km from the coast of Nova Scotia, south along longitude 63°25′W to the location of the shelf–slope water front. During May 1–6, 1977, this front was located approximately at 42°40′N, 24 km south from the shelf break, whereas during April 19–May 2, 1979, it was found at 42°28′N along 61°27′W about 126 km to the south of the shelf break. During June 4–6, 1978, stations for chlorophyll, temperature, and salinity were taken as far south as 42°05′N on 63°00′W with no evidence of the shelf–slope water front (Irwin and Platt 1979).

The sampling stations during each period were located from the edge of the continental shelf to water over the slope with a depth ranging up to 4000 m (Fig. 1). An attempt was made to establish stations in the shelf water, frontal zone, and the slope water mass.

All zooplankton and micronekton samples were taken with the BIONESS (Sameoto et al. 1980), which is a system of 10 opening and closing nets each with a mouth opening of 1 m^2. The mesh sizes of the nets used in 1977 were 243 μm and 1050 μm. Only the fine net samples were used to estimate zooplankton numbers while nets of both mesh sizes were used to gather the micronekton data. Because no significant difference was found in the number of species or size of micronekton caught in the two types of nets, only the 243-μm nets were used during the cruises in June 1978 and April 1979. These nets were fine enough to collect all zooplankton species over 300 μm in smallest dimension as well as micronekton up to 10 cm in length (Sameoto and Lewis 1980a, b). The BIONESS was towed at a speed of 1.5–2 m·s^{-1} as it was lowered along an oblique path to the desired depth. Nets were opened and closed on command at 5- to 10-m intervals in the euphotic zone (upper 40 m) and between 10- and 20-m intervals below this zone to the maximum depth sampled. The

volume of water sampled through each of the 10 nets ranged from 300 to 400 m^3. Most samples were taken during hours of darkness when the zooplankton and micronekton were concentrated in the top 150 m of water and less likely to avoid the net. In addition to collecting the biological material the BIONESS was equipped with a Guildline Instruments conductivity cell and temperature probe which collected salinity and temperature data simultaneously with the biological samples. The sampler also continuously monitored depth and flow through the nets. For a complete description of the BIONESS the reader is referred to Sameoto et al. (1980).

The samples were preserved in a 5% buffered formalin seawater solution. All the biomass values given are wet weight values obtained by weighing the animals after the free water was removed either by blotting the animals, as in the case of the micronekton (animals between 1 and 10 cm in length), or by vacuuming over a 100-μm filter in the case of the zooplankton (animals less than 1 cm in length). The zooplankton portion of the sample was split to ~200 animals using a Motoda splitter, and the species in the split were identified and counted. All the micronekton were identified and counted.

The energy value of zooplankton in kilojoules was determined using a Phillipson microbomb calorimeter. Live zooplankton were dried at 60°C for 24 h then weighed and stored in a desiccator before burning.

The calculation of biomass and numbers of animals/m^2 was made by calculating biomass and numbers/m^3 in each depth stratum sampled and then multiplying this value by the depth of the stratum. These values for all the sampled strata were added to give the total biomass and numbers/m^2 to the maximum depth sampled. Comparing the values/m^2 on different stations that were sampled to different depths was justified because it was observed from Batfish data that over 90% of the zooplankton population was confined to the top 40 m of water during the May 1977 cruise (Herman et al. 1981), and similar observations were made during the cruise on April 1979 (A. W. Herman, Atlantic Oceanography Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2, personal communication). In addition, the depth-stratified BIONESS samples and the acoustic data showed that during the night over 95% of the micronekton and zooplankton were concentrated in the top 50 m of water on the continental shelf stations and in the top 50–100 m in the region of deep water over the slope (Sameoto and Lewis 1980b).

Stomach contents of the euphausiids were examined following the method described by Sameoto (1980). The stomach contents of the myctophid *B. glaciale* were examined under a dissecting microscope after the fork length of the fish was measured. The contents were identified as to types of organisms present and their abundance. Fish were selected from a number of night stations from each of the cruises.

Acoustic Data Collection

A Simrad Scientific sounder model EK 120 R with a frequency of 120 kHz and transmitting sound level of 112 dB · $microbar^{-1}$ at 1 m was used throughout the study. The settings were held constant at 1 ms pulse length, 48 pulses per minute, a 9° beam width, and a bandwidth of 9.9 kHz. The transducer was mounted in a Braincon 0.6-m V-fin towed from the ship's side away from the ship's wake at a depth of 3 m. The acoustic echoes were recorded on echograms during all the BIONESS tows which provided a continuous record of the presence and vertical distribution of zooplankton and micronekton. In 1979 the echo sounder was operated along a north–south line from the shelf edge to the shelf–slope water front with the aim of determining the horizontal distribution of the zooplankton and the micronekton, and their relationship to the temperature and salinity in the shelf–slope water front region. At the same time continuous Batfish tows to record temperature, salinity, and chlorophyll were carried out (Herman and Dauphinee 1977).

Results

Acoustic Scattering Layers

Acoustic scattering layers in the top 150 m were found at night during all three cruises. The layers generally appeared in water where the bottom depth was 500 m or deeper and were continuous southward to the slope water front which was identified by the 12°C surface isotherm (Herman and Denman 1979; Herman et al. 1981). The temperature of the water in which the heaviest scattering layers were found ranged from 3°C near the surface to 11°C at ~150 m, and the salinity range was from a low of 30.48‰ near the surface to 35.75‰ at a depth of 150 m.

In May of 1977 the temperature on the slope (stn. 2, Fig. 1), where the water depth was 720 m, ranged from 12.0 to 14.0°C in the top 100 m. Scattering layers were very weak or absent in this water. The decreasing intensity of the layer is shown in Fig. 2. This was likely caused by the warming of the water from north to south which at 85 m was measured to change from 10 to 13°C. The decrease in the scattering intensity was not due to a downward migration of animals during the 30-min tow; the sounder detects the presence of animals down to 150 m and did not record animals moving downward.

The distribution and behavior of the acoustic scattering layers in April 1979 were similar to those observed in May 1977. There was intense backscattering in the top 150 m during the night from the region of the 1000-m contour on the slope south to the 12°C isotherm located at station 3 (Fig. 1). The intensity of the scattering layers at different depths was quite uniform with distance along each north–south transect in the slope water starting at the 1000-m-depth region, but quickly faded and disappeared as the ship entered the warmer water (temperatures above 12°C) of the shelf–slope water front (Fig. 2). The temperature and salinity profiles taken with the BIONESS showed that as the ship moved into the region of the slope water, the scattering was found mainly in the colder water which at the boundary lay on top of the slope water. The acoustic backscattering consisted of two primary layers, one between 0 and 50 m in depth and one between 75 and 125 m. The upper layer appeared to follow the 6°C contour and disappeared as this contour reached the surface (Fig. 3). The temperature contours influencing the deeper layer were less clear, but it appeared that the layer was found between 6 and 12°C and disappeared as the 12°C contour reached the surface. Most scattering layers disappeared at

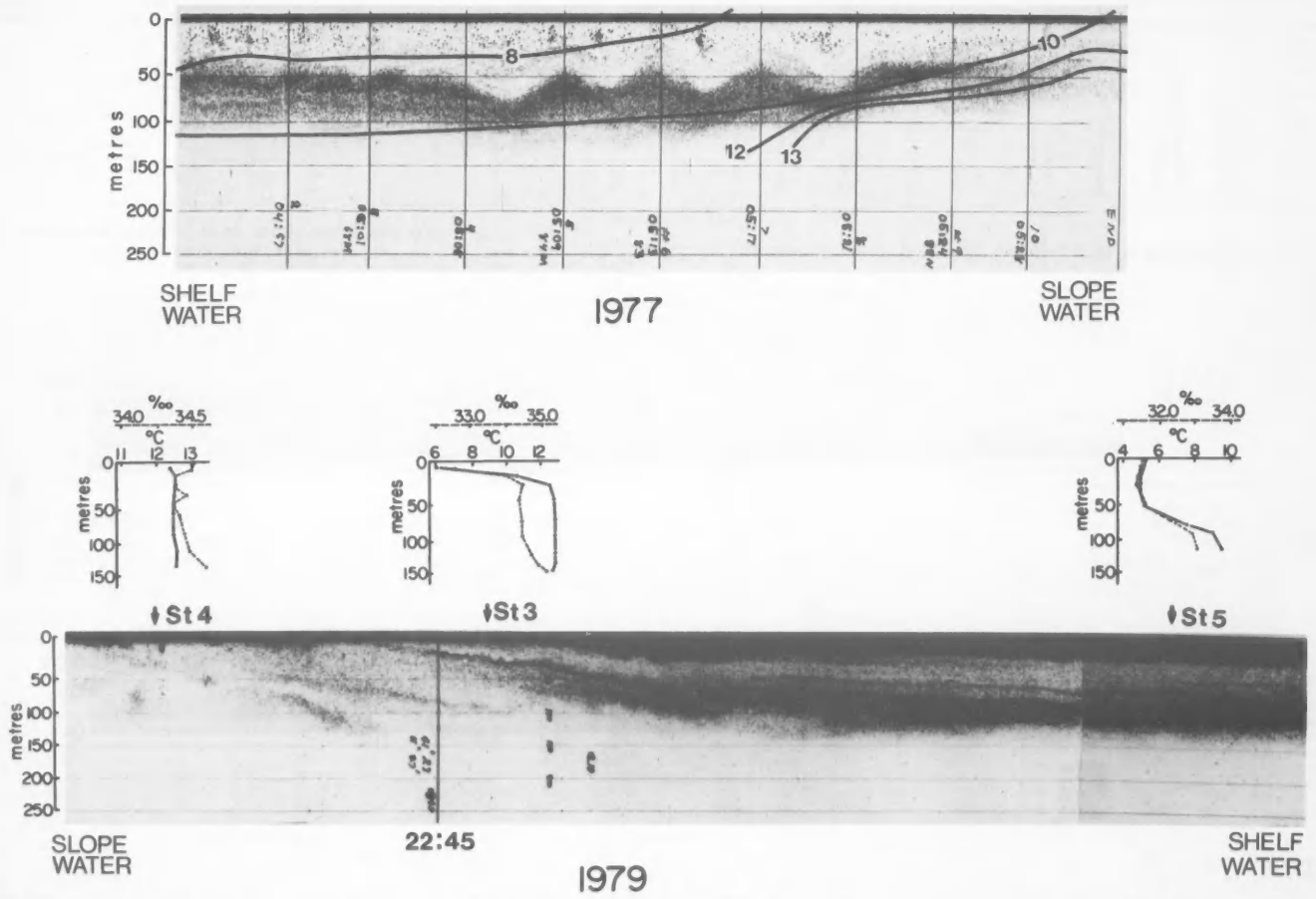


FIG. 2. *Top*: echograms of scattering layers seen north of the shelf–slope water front in May 1977. The vertical lines are starting positions of each BIONESS sample and are ~300–400 m apart. The temperature structure obtained from the BIONESS is shown. *Bottom*: Echogram north and south of the shelf–slope water front in April 1979, and the temperature and salinity profiles at three stations taken with BIONESS. Echogram was taken between 21:00 and 23:00, and the distance covered is ~20 km.

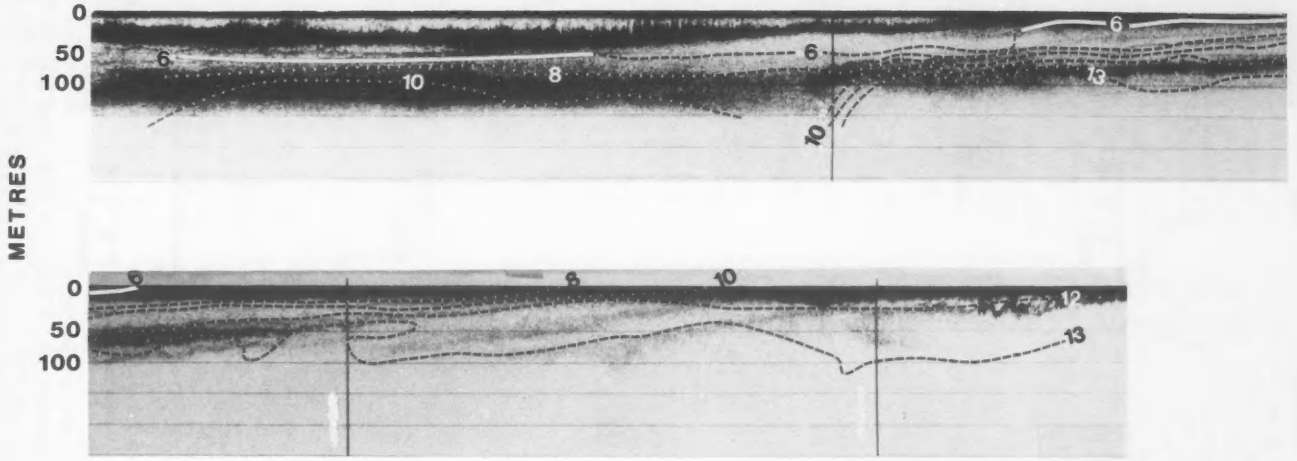


FIG. 3. Echogram of scattering layers between 01:00 and 03:00 on a north–south transect 23 km long through the shelf–slope water front showing the temperature structure as measured simultaneously by the Batfish during April 1979.

TABLE 1. Numbers of major groups of animals plus zooplankton and myctophid biomass $\cdot m^{-2}$ to the maximum depth sampled. Station numbers and bottom depths are given. Percentage of zooplankton biomass represented by euphausiid biomass and myctophid biomass plus temperature range of water sampled. All biomass values are wet weight estimates.

Stn. No.	Bottom depth (m)	Max. sample depth (m)	Urochordate	Cnidaria	Cephalopoda	Gastropoda	Ostracoda	Copepoda	Amphipoda	Euphausiacea[a]	Decapoda	Chaetognaths	Non-myctophid Osteichthyes	Myctophid larvae	Myctophid adults	Myctophid adults (g wet wt)	Zooplankton (< 1 cm) (g wet wt)	Euphausiacea[a] (g wet wt)	Myctophid biomass / Zooplankton biomass × 100	Euphausiid biomass / Zooplankton biomass × 100	Temperature range of water sampled
May 1977 Shelf water																					
9	144	45	1	7	0	210	43	51352	1	1090	16	134	3	0	0	0	19.3	0.75		0.03	5.9–9.1
1	144	78	0	1	0.5	15	15	15561	10	92	8	31	1	0.01	0	0.003	25.4	0.1		0.4	5.2–9.6
8	144	101	534	1	0.1	100	50	22798	83	619	0.1	258	2	0	0	0	13.7	0.42		0.07	5.9–10.9
7	162	124	6	1	0.1	110	20	98314	36	1324	33	163	4	0	0	0	28.6	0.1		0.3	6.1–10.0
4	360	32	0.03	0.01	0.5	16	3	34230	23	345	34	40	1	1	0	0	16.9	0.23			7.4–9.0
Slope water																					
6	720	87	0	0.01	0.1	3	87	15542	4	564	9	11	15	22	0.1	0.05	10.1	46	0.5	455	12.8–14.1
2	720	70	0.5	0.003	0.2	7	49	4225	10	92	2	13	2	0.02	0.14	0.14	9.9	0.1	1.4	1	8.8–13.2
2	1440	118	0.04		0.2	2	112	13093	8	658	5	13	5	7	0.3	0.25	4.8	23	5.2	479	7.2–12.4
3	1620	85	0.4	0.01	0.06	7	86	2432	1	165	23	30	5	11	0.3	0.17	6.5	14	2.6	215	10.0–13.0
Average values for shelf water (<12°C)			108	2	0.2			44451	31	694	18	125	2	0.2	0	0.0006	20.8	0.3		0.2	
Average values for slope water (>12°C)			0.2		0.1			8823	6	370	10	17	6	9.9	0.2	0.15	7.8	21	2.4	287	
June 1978 Shelf water																					
4	151	139	0	0.01	0	239	75	66748	1066	397	30	168	20		0	0	48.1	0.17	—	0.3	2.76–9.57
8	720	150	0	0.003	0	1061	5	123648	5157	238	10	101	2		0.2	0.1	82.3	1.9	0.1	2	4.80–10.02
5[b]	1260	150	0	0.004	0	3832	5	34306	2439	245	0	100	4		5	2.0	45.1	3.9	4.4	9	4.94–8.56
7	1260	130	0	0.003	0	4441	7	109968	8159	561	5	182	23		9	5.3	113.0	11.5	4.7	10	4.76–9.50
1	1260	175	0	0.003	0	974	6	58952	5212	1629	0.7	38	0		13	5.8	59.5	2.1	9.7	3	3.16–11.41
3	1440	200	0	0.01	0.13	424	26	39234	4069	1444	6	120	0		5	2.6	67.6	11.7	3.8	17	4.05–10.72
Average values					0.02	1828	19	72143	4350	752	9	118	9		6	3.2	69.3	5.2	4.5	7	
April 1979 Shelf water																					
1	300	180	9	3	0.4	1563	1314	52342	66	6344	0.4	752	0.9	0.3	0	0.008	20.6	3.9	0.04	19	3.87–10.05
11	400	160	0.3	2	0.1	1617	542	85092	51	1117	3	225	0.03	0.4	2.6	1.83	28.0	5.7	7	20	4.26–9.54
10	1300	150	0.5	24	0.1	1039	674	46960	3	6210	6	1881	0.5	0.2	1.8	1.77	17.9	2.1	10	12	5.00–9.94
9	2100	150	1	9	0.5	1359	663	42166	116	1790	5	329	2.0	1	5	2.82	15.0	3.2	19	21	5.37–10.06
8	2300	160	57	21	0.2	1886	1508	40526	252	3136	1	1034	0.3	11	0	0.02	20.1	0.07		0.3	5.07–10.09
12	3000	428	641	58	0.3	4625	716	77752	308	8610	14	2569	0.6	7	2	1.25	43.6	2.0	3	5	4.54–9.70
7	4140	150	4642	14	0.1	15765	2156	35629	381	5600	2	763	0.1	6	3	1.47	22.0	2.2	7	10	6.07–10.68
6	4140	160	122	2	0	3561	695	10864	24	1751	0.5	611	0	0.01	0	0	10.3	0.004		0.04	5.17–10.27
2	4200	150	18	9	0	5162	552	42361	166	2275	0	760	0.1	0.3	0	1.32	22.9	0.004	6	0.02	4.75–8.64
5	4200	150	95	5	0.5	4071	1434	50473	125	6945	18	786	0.4	1.4	2.6	0.004	18.0	2.5	0.02	14	5.66–10.54
Slope water																					
3	4300	150	6	25	1.1	1359	801	17984	47	3407	7	425	0.9	36	0	0.04	5.3[c]	0.1	0.7	2	6.02–12.86
4	4320	150	7	12	0.1	472	1383	29330	29	2089	10	365	0.3	64	0.1	0.31	9.5	2.1	3	22	12.47–12.60
Average values for shelf water (<12°C)			559	15	0.2	4065	1025	48416	149	4377	5	971	0.5	2.8	1.7	1.31[c]	21.8	2.2	7	13	
Average values for slope water (>12°C)			6	18	0.6	915	1092	23657	38	2748	9	395	0.4	50	0.1	0.31[c]	7.4	1.1	3	12	

[a]Euphausiacea collected in shelf water and station 2 in May 1977 were all calyptopis and furciliae stages which accounts for the very low biomass.
[b]Samples from the top 55 m were lost, therefore these values are likely underestimated.
[c]Day time stations 3, 6, and 8 excluded from mean estimate.

TABLE 2. Dominant species represented as % of individuals in each group during sampling period from May 1 to 6, 1977, April 19 to May 2, 1979, and June 4 to 6, 1978.

	May 1–6, 1977				April 19–May 2, 1979				June 4–6, 1978	
Group	Shelf water	%	Slope water	%	Shelf water	%	Slope water	%	Shelf water	%
Gastropoda	*Limacina retroversa* *Limacina* sp.	50 50	*Limacina retroversa*	100	*Limacina trochiformis*	99	*Limacina trochiformis* *Euclio* sp.	63 25	*Limacina retroversa* *Clione* sp.	91 26
Ostracoda			*Halocypris globosa*	81	*Conchoecia elegans* *C. haddoni*	58 26	*Conchoecia haddoni* *C. obtusata* *Halocypris globosa* *Pleuromamma borealis*	19 30 28 36		
Copepoda	*Calanus finmarchicus* *Clausocalanus* sp.	90 5	*Metridia lucens* *Pleuromamma borealis* *P. robusta* *Calanus finmarchicus*	42 30 15 9	*Calanus finmarchicus* *Clausocalanus arcuicornis* *Metridia lucens* *Pleuromamma borealis*	42 2 35 3	*Clausocalanus arcuicornis* *Metridia lucens* *C. finmarchicus*	25 15 2	*C. finmarchicus* *M. lucens*	90 5
	Amphipoda	—	*Unciola irrata*	100	*Parathemisto* sp.	99	*Parathemisto* sp.	99	*Parathemisto* sp.	90
Euphausiacea	*Thysanoessa* calyptosis *T.* furciliae	32 67	*Thysanoessa* calyptosis	87	*Thysanoessa longicaudata*	99	*Thysanoessa longicaudata* *Stylocheiron* sp.	88 5	*Meganyctiphanes norvegica* *T. longicaudata*	30 70
Chaetognatha	*Sagitta* sp. *Eukronia hamata*	70	*Eukronia hamata*	79	*Sagitta* sp. *Eukronia hamata*	62 21	*Sagitta* sp.	53	*Sagitta* sp.	70
Urochordata	Salpidae	100	Salpidae	100	*Oikopleura vanoeffeni*	99	*Salpa* sp.	100	Ascidacea	100
Osteichthyes	*Merluccius bilinearis*	95	*Benthosema glaciale*	67	*Benthosema glaciale*	96	Myctophid larvae (*Benthosema* sp.)	98	*Benthosema glaciale*	90
Decapoda	Unidentified zoea	90	Brachyura zoea	98	*Sergestes arcticus*	90	*S. arcticus*	70	*S. arcticus*	70

sunrise, with the only layer remaining being the one in the top 50 m at a much reduced intensity.

The scattering layers in April 1979 over the deeper parts of the slope (over 1000 m) were not seen in the shallower regions even though there was no obvious difference in temperature and structure of the water. Tows up to 36 km in length showed very little change in the intensity of the layers at the different depths. This suggested a relative uniform distribution of animals in the shelf water between the 1000-m contour and the shelf–slope water front. The BIONESS samples in 1979 confirmed this uniformity in distribution.

The animals causing much of the backscattering were probably migrators (such as myctophids and euphausiids) that descended into deep water during the daytime, because almost none of these animals were caught during the day (Sameoto and Lewis 1980a, b).

In June 1978, the pattern of acoustic scattering layers in the deep slope region was similar to the two spring cruises, being present once the water depth reached 1000 m and were continuous to the most southerly station located in 1620 m of water at 42°30′N. The intensity of the layers at night was greater than those seen during the spring cruises (Sameoto and Lewis 1980b), and as in the case of the spring cruises, the layers disappeared at sunrise. The pattern of the scattering layers was the same as seen in April with two main layers present, one between 0 and 50 m and one from 75 to 125 m. The shelf–slope water front was not located during this cruise even though the most southerly station was located at 42°05′N (Irwin and Platt 1979). At this station the 12°C contour appeared at a depth of 90 m indicating that the slope water front was near. At this station there were only very weak acoustic scattering layers following the pattern of the other two periods.

A comparison between the presence of acoustic scattering layers and the numbers of micronekton of various species $\cdot m^{-3}$ at the depths of the layers showed that the scattering layers were probably due mainly to the micronekton (Sameoto and Lewis 1980b). The copeods produced visible scattering layers only at high densities (i.e. $>1000 \cdot m^{-3}$, Sameoto and Lewis 1980b) as was generally found in the top 50 m of water. Therefore, in most cases the upper scattering layer between 0 and 50 m was probably due in large part to copepods, euphausiids, and myctophids whereas the lower layer was due primarily to myctophids. This is in agreement with Halliday (1970), who found *B. glaciale* to be centered between 45 and 90 m during the night. But because of a lack of data on the target strengths of the different species, it was impossible to state definitely that one or another group of animals was the main acoustic scatterer.

Zooplankton and Micronekton Numbers and Biomass

The zooplankton biomass/m^2 in shelf water during May 1977 only varied by a factor of 2 on the different stations. Similar between-station variability was found in the slope water even though the average biomass of zooplankton was much lower there (Table 1). A decrease in biomass/m^2 occurred as the stations entered the warmer shelf–slope frontal region. The most southerly station, No. 3, and the one in the warmest water (between 10 and 13°C) had the lowest number of copepods/m^2, about an order of magnitude lower than was found in the shelf water (Table 1). The decrease in biomass/m^2 in the warmer water was due primarily to fewer copepods associated with water of 12°C or greater. This effect was also seen in the echogram of stations entering the frontal zone which showed the number of acoustic scatters decreased as the zone of 13°C water was entered (Fig. 2).

The dominant copepod species on stations north of the shelf–slope front (water <12°C) during May 1977 were *Calanus finmarchicus* and *Clausocalanus* sp. which represented 90 and 5% of the total copepod population, respectively (Table 2). In the warmer slope water, numbers of these species dropped dramatically, with *C. finmarchicus* making up only 9% of the total population. No single species totally dominated the copepods in the slope water, but the most abundant species were *Metridia lucens* which made up 42% of the population, with *Pleuromamma borealis* and *P. robusta* making up 30 and 15% of the population.

The euphausiid biomass made up of adult *Megancytiphanes norvegica* and *Thysanoessa longicaudata* increased in the warmer frontal waters and on three of the four stations had a greater biomass than the other zooplankton (Table 1). The high numbers of euphausiids/m^2 in the shelf water were due to calyptopis and furcilia stages of *Thysanoessa* sp. which were less than 1 cm long and therefore did not represent a large biomass.

Salps were abundant on only one station in the shelf water (Table 1) and were not a significant component of the zooplankton in the frontal zone (Table 1). The chaetognaths, mainly *Eukronia hamata*, were much more abundant in the shelf water where the bottom depth was less than 360 m than they were in the area of the front. The cnidaria group was insignificant in numbers and biomass on all stations in both the shelf and frontal zone.

The abundance of non-myctophid larval fish was greater in the slope water than in the shelf water (Table 1), with the dominant species being *Sebastes marinus*. In the shelf water the dominant species of larval fish was *Merluccius bilinearis*.

Myctophid larvae and adults dominated the fish population in the slope water in terms of both numbers and biomass and were the most important component of the micronekton next to the euphausiids. *Benthosema glaciale* was the dominant species of myctophid representing 67% of the individuals caught. Other species of mytophids caught in the warmer water of the frontal zone were *Lampanyctus alatus*, *Benthosema suborbitale*, *Diogenichthys atlanticus*, *Notolychnus valdiviae*, *Bolinichthys indicus*, and *Ceratoscopelus maderensis*.

Other common micronekton found in 1977 were the decapod shrimps, mainly *Sergestes arcticus*, and cephalopods, primarily the squids *Illex illecebrosus* and *Megalochranchia* sp. The numbers of these groups were similar in both the shelf and slope water regions (Table 1).

The results from April 1979 provided some interesting similarities and differences with the 1977 species abundance and biomass values. The average zooplankton biomass/m^2 in the shelf water, identified as water 11°C or less, and the slope water, over 12°C, were strikingly similar in the 2 yr. In 1977, the shelf water average biomass was 20.8 g wet weight/m^2 and in 1979 it was 21.8 g/m^2, while in the slope-water zone during these years it was 7.8 g and 7.4 g, respectively. In 1979 the zooplankton in the shelf water was domi-

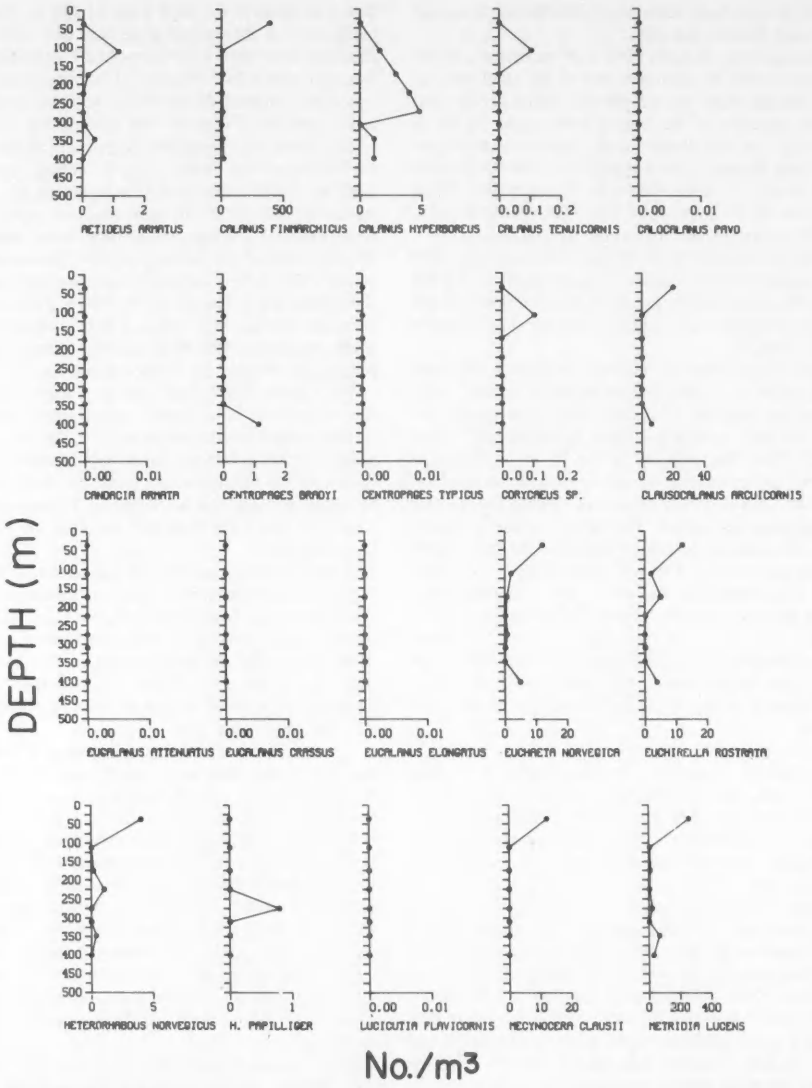
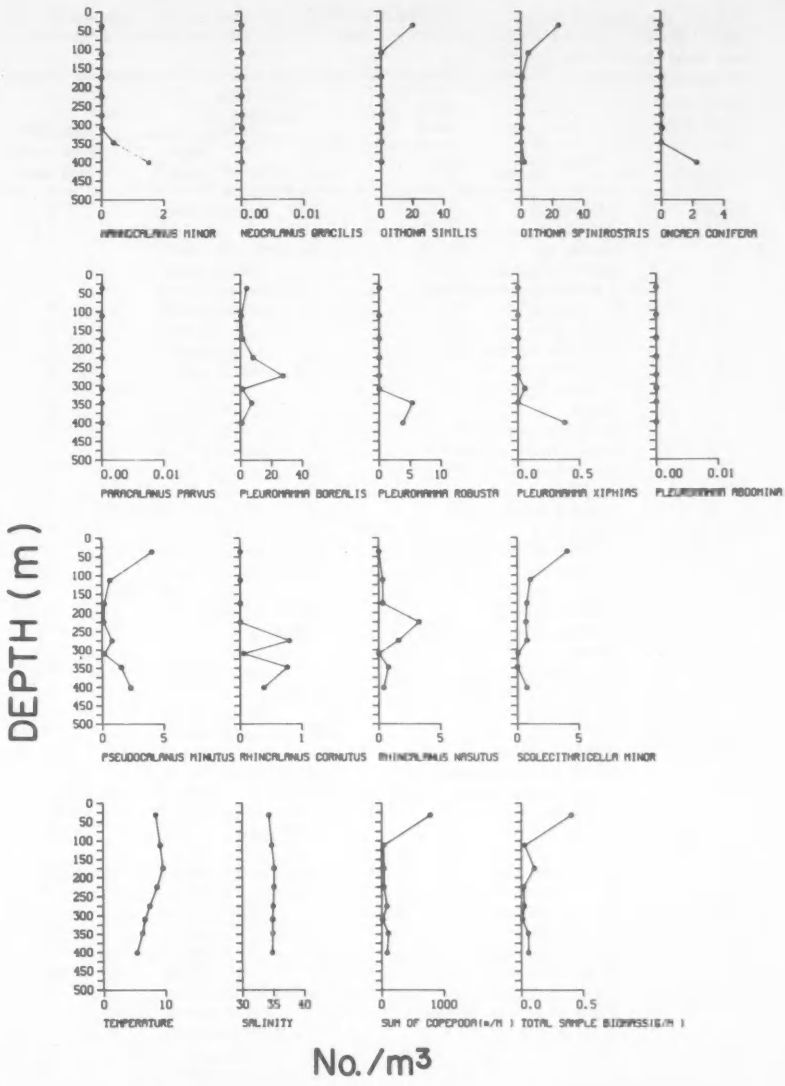


FIG. 4. Vertical distribution of copepods at station 12 sampled at 15:00 May 2, 1979. Each point is the mean number/m^3 located at the

nated by *C. finmarchicus* as it was in 1977, but *Metridia lucens* replaced *Clausocalanus* sp. as the second most abundant species (Table 2). The most numerous species of copepods in the slope water were *P. borealis* and *Clausocalanus arcuicornis* with *C. finmarchicus* representing only 2% of the total number of copepods (Table 2). Most euphausiids on all stations were calyptosis and furcilia stages of *T. longicaudata* with few adults present. To verify that most copepods in 1979 were within the upper 75 m of water as was shown by the acoustic and Batfish data (Herman personal communication), a BIONESS tow was made to a depth of 428 m (stn. 12). This tow showed no significant numbers or biomass of copepods below 75 m during the day when the population of diurnal migrating copepods is the greatest at lower depths (Fig. 4). This was not surprising because the ontogenetic migration of *C. finmarchicus* occurs in March and early April (Marshall and Orr 1955). *Pleuromamma borealis* was the most abundant copepod below 75 m and its numbers were insignificant compared to the total number of copepods above 75 m.

The main difference in the zooplankton and micronekton



mid-depth of the sampled strata. The mean temperature, salinity, and biomass of zooplankton are shown for each sampled stratum.

between 1979 and 1977 was the greater abundance of all groups of animals other than the copepods in 1979 (Table 1) compared with 1977. It was unlikely that the deeper depth sampled at night in 1979 contributed very much to the increase in animal abundance because the vast majority of animals of all groups were caught in the upper 75 m during the night in 1977 (Sameoto and Lewis 1980a, Herman et al. 1981).

The amphipods, cnidaria, ctenophores, and chaetognaths numbers/m^2 were relatively low compared to the other groups of animals (Table 1) and therefore were likely insignificant predators on the zooplankton. The urochordata, primarily the larvacean *Oikopleura vanhoeffeni*, were abundant only on one station in the shelf water (Table 1).

The myctophid numbers and biomass/m^2 were higher by at least an order of magnitude in 1979 compared with 1977 (Table 1) with *B. glaciale* making up 90% of the myctophids caught (Table 3). The numbers and biomass of myctophids on the different stations sampled at night in the shelf water were very similar (Table 1) suggesting a relatively uniform

TABLE 3. List of species in each group collected in shelf and slope waters plus their mean numbers per square metre for all stations sampled April 1979 and June 1978. Species marked with an asterisk (*) were only found in slope water in April.

Group	Species	April 1979, mean No./m^2		June 1978, mean No./m^2
		Shelf water	Slope water	shelf water
Cnidaria	*Ablopsis* sp.	0.05	0.1	0
	Agalma elegans	0.01	0.05	1.5
	**Agalma* sp.	0	0.05	0
	**Aglantha digitale*	0	0.2	0
	Chelophyes appendiculata	0.6	0.9	3
	**C. contorta*	0	0.05	0
	Chelophyes sp.	0.02	0.05	0
	Dimophyes arctica	0.5	0.7	0.4
	Dimophyes sp.	0.1	0	0
	**Diphyes dispar*	0	0.1	0
	**Diphyes* sp.	0	0.1	0
	**Eudoxoides spiralis*	0	0.05	0
	Hippopodius hippopus	1	0.05	0
	Lensia conoidea	0	1	0.01
	Lensia sp.	0.8	5	0
	Nanomia cara	2	0	0.01
	Nanomia sp.	1	0	0
	Physophora sp.	0.01	0	0
	Stephanomia	0	0	0.8
	**Sulculeolaria chuni*	0	0.05	0
	Sulculeolaria sp.	0	2	0
	Hydromedusae	3	3	0
	Medusae	0.1	1	0.2
	**Cyanea* sp.	0	0.05	0
	Periphylla periphylla	0.02	0	0
	Pelagiidae sp.	2	4	0
Copepoda	*Aetideus armatus*	318	159	18
	Amallothrix emarginata	0.6	0	0
	Calanus finmarchicus	26466	556	58110
	C. hyperboreus	378	18	1468
	C. glacialis	0	0	349
	C. tenuicornis	4	31	0
	**Calocalanus pavo*	0	24	0
	**C. plumulosus*	0	18	0
	Candacia armata	8	50	2
	**C. longimana*	0	5	0
	**Centropages bradyi*	6	94	0
	C. typicus	29	122	0
	Chirundius streetsii	0	0	1
	Clausocalanus arcuicornis	807	4461	1
	Corycaeus sp.	15	70	0
	Eucalanus attenuatus	67	29	0
	**E. crassus*	0	30	0
	E. elongatus	5	21	0
	Euchaeta acuta	2	0	0
	E. norvegica	1577	1000	276
	E. withii	0	25	0
	Euchirella messinensis	0	8	0
	E. rostrata	1746	2273	164
	Gaidus tenuispinus	8	0	3
	Haloptilus acutifrons	0	4	0
	H. longicornis	6	19	0
	Heterorhabdus abyssalis	0	3	0
	H. norvegicus	105	95	20
	H. pappilliger	4	13	0
	Lucicutia flavicornis	21	198	0

TABLE 3. (*Continued*)

Group	Species	April 1979, mean No./m²		June 1978, mean No./m²
		Shelf water	Slope water	shelf water
	Mecynocera clausii	105	366	0
	Metridia sp. immature	0	0	2920
	Metridia longa	0	0	1605
	M. lucens	10797	5203	2062
	**Microstella norvegica*	0	8	0
	Nannocalanus minor	29	252	21
	Neocalanus gracilis	4	165	0
	Oithona atlantica	0	0	214
	O. similis	207	56	0
	O. spinirostris	1236	1077	0
	Oncaea conifera	31	177	0.3
	O. venusta	0	0	0.1
	Paracalanus parvus	3	25	
	Pleuromamma sp.	0	0	22
	P. abdominalis	118	182	0
	P. borealis	690	5643	40
	**P. gracilis*	0	13	0
	P. robusta	78	84	102
	P. xiphias	8	11	0.02
	Pseudocalanus minutus	580	85	3751
	Rhincalanus cornutus	15	13	0
	R. nasutus	45	79	2
	Rhincalanus sp.	0	0	1
	Scolecithricella minor	632	98	972
	Scolecithricella sp.	0	0	3
	Scolecithrix bradyi	4	6	0
	**S. danae*	0	25	0
	Scolecithrix sp.	1	0	0
	Scottocalanus persecans	0	0	0.02
	S. securifrons	0	5	0
	Temora longicornis	2	4	0
	Tisbe sp.	0	0	9
	Undeuchaeta minor	0	8	0
	Undeuchaeta plumosa	2	0	0
Amphipoda	*Ampelisca mexicana*	0	0	0.4
	Eurythenes obesus	0	0	0.02
	Hyperia galba	0	0.1	0
	**Hyperia medusarum*	0	0	0
	H. spinigera	0	0	0
	Hyperia sp.	0	0.05	0
	Hyperoche medusarum	0.2	0	0
	Oxycephalus sp.	0	0	0
	Parathemisto abyssorum	0	0	0
	P. gaudichaudii	8	1	354
	Parathemisto sp.	140	36	3992
	**Phronima atlantica*	0	0.05	0
	**P. sedentaria*	0	0.05	0
	**Phronima* sp.	0	0.1	0
	**Phrosina semilunata*	0	0.05	0
	Physomata sp.	0.05	0	0
	Scina borealis	0.1	0	0
	Vibilia sp.	0.01	0.2	0
	Gammariidae	<0.01	0	0.02
	**Orchomella* sp.	0	0.05	0
	**Rhabdosoma* sp.	0	0.05	0
Euphausiacea	*Euphausia krohni*	6	29	180
	Euphausia sp.	0.2	4	0

TABLE 3. (*Continued*)

Group	Species	April 1979, mean No./m²		June 1978, mean No./m²
		Shelf water	Slope water	shelf water
	Meganyctiphanes norvegica	8	0.05	91
	Nematoscelis megalops	7	10	11
	Thysanoessa calyptopis	2324	2015	0
	T. furciliae	1710	380	0
	T. longicaudata	310	197	454
	T. inermis	0	0	0.2
	T. raschii	0	0	0.02
	T. acutifrons	0	0	1
	Stylocheiron maximum	0	0	0.05
Decapoda	*Acanthephyra* sp.	0	0	0.02
	Acanthephyra pelagica	0	0	0.02
	**Brachyura* larvae	0	0.1	0
	Caridion sp.	0	0	5
	Gennadas elegans	0.1	0.05	0.01
	G. valens	0	0	0.01
	Pandalus montagui	0	0	0.02
	**Palinurus* sp.	0.1	0.05	0
	Pontophilus norvegica	0	0	2
	Sergestes sp. immature	3	5	2
	S. arcticus	1	0.05	0.01
	**S. henseni*	0	0.05	0
	**S. pectinatus*	0	0.05	0
	Solenocera sp.	0.4	0.1	0.02
	Spirocantaris sp.	0	0	0.02
	Unidentified larvae	0.2	1	0
	Lucifer sp.	0.01	2	0
Chaetognatha	Unidentified	223	171	44
	Eukronia fowleri	0	0	2
	E. hamata	145	61	12
	Sagitta elegans	7	0	25
	S. macrocephala	1	15	0
	Sagitta sp.	183	147	0
	S. maxima	0	0	6
	S. tasmanica	0	0	27
Urochordata	Ascidiacea	0	0	0.01
	Oikopleura vanhoeffeni	552	3	0
	Oikopleura sp.	6	0	0
	Salpa fusiformis	2	3	0
Ctenophora	*Beroe* sp.	0.1	0.1	0
	Pleurobrachia sp.	0.02	0.05	0
	**P. pileus*	0.02	0.1	0
	**Mertensia ovum*	0.02	0	0
	Bolinopsis sp.	0	0.5	0
	Unidentified	0	0	0.1
Gastropoda	*Clione* sp.	3	0	1077
	C. limacina	0	0	3
	Euclio pyramidata	3	28	0
	Euclio sp.	38	58	0
	Limacina helicina	0	0	10
	L. retroversa	264	3	719
	L. trochiformis	3756	826	0
	Paedoclione dolioformis	0	0	19
Cephalopoda	*Megalocranchia* sp.	0.2	0.6	0

TABLE 3. *(Concluded)*

Group	Species	April 1979, mean No./m^2		June 1978, mean No./m^2
		Shelf water	Slope water	shelf water
	Illex illecebrosus	0.2	0.1	0.02
	**Octopus*	0	0.1	0
Polychaeta	Unidentified	0.1	0	0
	Tomopteris sp.	3	2	0
	T. septentrionalis	4	0	0
	Spiophanes sp.	0	0	1.2
Ostracoda	*Conchoecia acuticosta*	0	0	8
	C. curta	58	80	0
	C. daphaenoides	1	0	0
	C. elegans	313	91	6
	C. haddoni	273	292	0
	C. obtusata	360	282	4
	Halocypris brevirostris	4	0	0
	Halocypris globosa	7	292	0
	Fellia sp.	1	24	0
	Unidentified	5	30	0
Osteichthyes	*Ammodytes* sp.	6	0	1
	A. tobianus	0	0	5
	Anarhichas sp.	0	0	0.05
	**Anguilla rostrata*	0	0.03	0
	Barrucudina	0	0	0.02
	Conger sp.	0	<0.01	0
	Cyclothone sp.	2	0	0
	Gadidae sp.	0	0	1
	Merluccius bilinearis	0.04	0	0.01
	Myctophidae:			
	Immature myctophid	2	49	0
	Benthosema glaciale (adults)	2	0.04	6
	Nemichthyes scolopaceus	0	0	0.02
	Primnothorus	0	0	0.1

distribution. The day stations had much lower numbers of myctophids because they are found at depths over 300 m during the day (Halliday 1970) and therefore except for station 12 were out of range of the nets. For this reason the day station values were not included in the averages for numbers and biomass/m^2. The average biomass/m^2 of myctophids was much higher in the shelf water because most were adults while most myctophids in the slope water were larvae (Table 1).

The most southerly station in the slope water in 1979 had low numbers of the myctophids *Certoscopeleus maderensis*, *Diaphus rafinesquei*, *N. valdiviae*, *Hygophum hygomii*, *Symbolophorus verany*, and *D. atlanticus*. These species were not found in the shelf water.

In June 1978, one station was sampled on the Nova Scotian shelf and five on the slope (Fig. 1), but all stations were in shelf water as based on the temperature range (Table 1). There was no noticeable difference in the species composition of zooplankton and micronekton on the shelf and slope stations other than the larger number and biomass/m^2 of myctophids on the slope. The zooplankton were dominated by two species of copepods, *C. finmarchicus* and *M. lucens* (Table 2 and 3), as in the earlier studies. The numbers of copepods/m^2 were ~1.6 times higher in 1978 than in the 1977 and 1979 spring periods, but the zooplankton biomass/m^2 was over 3 times as great in June as a result of the large number of juvenile hyperiid amphipods, *Parathemisto* sp., and the dominance of large *C. finmarchicus* individuals.

The salps, cnidaria, and cephalopods were an insignificant component of the samples in 1978 (Table 3). The chaetognath numbers were intermediate between those found in 1977 and 1978 (Table 1). The decapods, mainly *Caridon* sp. (Table 3), were similar in abundance to the other studies. The most significant difference in the micronekton was the abundance of the myctophid *B. glaciale* which had about 3 times more biomass/m^2 than in 1979 and 30 times more than in 1977 (Table 1).

The dominant micronekton on the slope other than the myctophids were the euphausiids *M. norvegica* and *T. longicaudata* and the hyperiid amphipods *Parathemisto gaudichaudi* and *Parathemisto* sp. (Table 3). These animals and *B. glaciale* were considered to be responsible for the intense acoustic scattering layers seen off the edge of the shelf

TABLE 4. The number of species in each animal group on the different stations in shelf and slope water during April 1979, and the numbers of species found on all stations in June 1978.

Station No.	Cnidaria	Ctenophora	Gastropoda	Cephalopoda	Polychaeta	Ostracoda	Copepoda	Amphipoda	Euphausiacea	Decapoda	Chaetognatha	Urochordata	Osteichthyes	Total no. of species
	Number of species													
	April 1979													
Shelf water														
1	3	1	3	0	2	6	18	3	5	3	4	1	5	54
9	4	2	5	2	2	8	25	7	6	4	4	1	5	75
8	8	2	3	1	2	6	23	3	6	2	3	1	2	62
7	8	2	4	1	1	6	22	6	9	5	4	2	5	75
6	4	1	2	1	1	4	18	5	3	2	4	1	1	47
2	4	3	2	0	1	3	14	3	2	0	4	1	2	39
5	9	3	2	2	2	5	24	6	8	6	4	4	5	80
Slope water														
3	23	4	3	3	2	5	35	11	6	5	3	1	8	109
4	15	5	3	1	2	7	42	8	11	10	4	2	12	122
	June 1978													
Shelf water	7	1	5	1	2	4	29	6	9	10	7	1	11	93

(Sameoto and Lewis 1980b).

The dominant non-myctophid fish larvae on all the stations on the shelf and slope were *Ammodytes tobianus*, whereas the larvae of *B. glaciale* were the dominant species of fish larvae on the stations over the slope (Table 3).

SHELF AND SLOPE WATER SPECIES COMPOSITION

The 1979 data showed 41 additional species present in the slope water that were not found on any of the colder shelf water stations (Table 3), whereas none were found only in the shelf water. The number of species in each group remained relatively constant along the north–south line of stations in the shelf water in April 1979, but once the slope water was reached the numbers of species in the groups Copepoda, Cnidaria, and Osteichthyes increased significantly (Tables 3 and 4). It was these three groups that contributed most to the increased species diversity in the slope water.

More species in each group occurred in April 1979, particularly in the copepods and cnidaria (Table 3 and 4) than in June 1978. Only six species of copepods found in June were not found in April, but none found only in the slope water in April were found in the shelf water in June (Table 3). The group with the greatest change in its species composition in June was Osteichthyes with 6 out of 13 species not found in April (Table 3).

The drop in zooplankton biomass between the shelf and slope water was due mainly to the reduction in the numbers of *C. finmarchicus* in slope water. All the other species of copepods found in the shelf water were also found in the slope water, at densities similar to that in shelf water. The presence of the front did not seem to have a significant effect on the species composition or numbers of euphausiids. The groups of micronekton that were affected by the front were the myctophids and cnidaria. The numbers of *B. graciale* were significantly lower in the slope water than in shelf water which supported Hallidays' (1970) suggestion that *B. glaciale* is found in water of less than 15.6°C. The number of other species of myctophids increased in slope water although the total numbers of myctophids was much lower than in the shelf water.

The numbers of cnidaria species rose in the slope water, but the total number of individuals/m^2 did not increase over the mean number found in the shelf water. Therefore what was seen was a community of animals in the slope water that was more diverse with respect to the total number of species, but other than the copepods did not differ greatly in the number of animals/m^2.

PREDATION BY EUPHAUSIIDS AND MYCTOPHIDS

The stomach contents of 35 adult *M. norvegica* were examined from night stations taken during each of the sample periods. The results showed that 98% contained copepod remains which made up about 90% of the volume of material in the stomachs. Plant material was also common with the most abundant being the dinoflagellates *Peridinium* and *Ceratium*, but these cells were a very small part of the total volume of the stomach contents. The stomachs of 20 *T. longicaudata* showed only crustacean remains which were primarily from copepods. The stomachs of 20 *B. glaciale* ranging in fork length from 30 to 56 mm all contained copepods with the most common one being *C. finmarchicus* which made up over 90% of the stomach volumes. *Pleuromamma*, *Metridia*, and

TABLE 5. Mean biomass estimates of kJ/m^2 in shelf and slope water for zooplankton, euphausiids and myctophids, and the daily consumption of zooplankton in kJ by euphausiids and myctophids.

	Shelf water			Slope water	
	May 1977	April 1979	June 1978	May 1977	April 1979
Zooplankton					
Dry wt[a]	3.1	3.3	10.4	1.2	1.1
kJ[b]	71.2	75.8	239.4	27.6	25.1
Euphausiids					
Dry wt[c]	0.009	0.5	1.2	4.6	0.2
kJ[d]	1.7	16.3	23.4	94.2	5.0
Daily consumption of zooplankton (kJ)	0.08	0.8	0.9	3.8	0.2
Daily consumption as % of zooplankton (kJ)	0.1	1.0	0.4	14	1.8
Myctophids					
Wet wt	0.0006	1.3	3.2	0.15	0.2
kJ[e]	0.003	7.1	17.6	0.8	1.3
Daily consumption of zooplankton (kJ)[f]		0.1	0.2	0.01	0.01
Daily consumption as % of zooplankton (kJ)		0.1	0.1	0.03	0.04
Total % consumed by euphausiids and myctophids	0.1	1.1	0.5	14.0	0.84

[a]Dry weight measured to be 15 ± 2% of wet weight.
[b]Measured to be 23 ± 0.4 kJ per gram dry weight for zooplankton dominated by *C. finmarchius*.
[c]Measured to be 22 ± 2% of wet weight.
[d]One gram dry weight = 20.5 kJ (Sameoto 1976).
[e]Based on 1 g wet weight flesh = 5.4 kJ (Banse and Mosher 1980).
[f]Childress et al. 1980.

small euphausiids were also found but in low numbers. These findings agreed with those of Gjosaeter (1973), who found *B. glaciale* fed primarily on copepods. Diatom cells were found in about 10% of the animals examined, but the volume of this material was insignificant. These data for the euphausiids and myctophids showed that the two groups were major predators on copepods during all three study periods.

The euphausiids were estimated to consume a higher percentage of the copepod energy than the myctophids during all three sampling periods. In 1977 euphausiids consumed 0.1% per day of the copepod energy in the shelf water and 14% in the slope water (Table 5). This difference was the result of very few adult euphausiids being found in the shelf water. The high percent consumption in the slope water, the result of their high biomass, suggests that the euphausiids could have easily destroyed the copepod population in this region with time if the production rate of copepods was not equal to, or greater than, 14% per day.

The consumption of copepods by euphausiids in the slope water was also higher than in the shelf water in April 1979, because of a proportionately higher biomass of euphausiids than copepods in the slope water. But the daily consumption (0.8%) was much lower than estimated for May 1977.

In June 1978 the biomass of both the copepods and euphausiids was higher than during the April sampling period, but the percent consumption of copepods by the euphausiids was similar to April (Table 5).

During both April 1979 and June 1978 the consumption of copepods by the myctophid population was similar, about 0.1% of the copepod energy per day, even though the biomass/m^2 of both the copepods and myctophids was higher in June. In the slope water the consumption was an order of magnitude lower than it was in the shelf water during both 1977 and 1979. This was the result of a proportionately greater drop in the biomass of myctophids than for the biomass of copepods in the slope water.

Discussion

The dominant zooplankton predators in both the shelf and slope waters were the myctophid *B. glaciale* and the euphausiids *M. norvegica* and *T. longicaudata*. The daily total consumption estimates in kilojoules of zooplankton energy by these two groups of animals in the shelf water was a much smaller percentage of the total zooplankton energy than in the slope water during 1977 due to the absence of adult euphausiids and myctophids in the shelf water. In 1979 the percent consumption by the two groups combined was very similar in the two water masses even though the biomass of zooplankton, euphausiids, and myctophids was each lower in the slope water. The impact of predation on the zooplankton population must have been great particularly when there were large numbers of euphausiids present as in the slope water in 1977. The yearly P/B ratio of zooplankton in the two water masses would have to be greater than 3 just to provide the energy for these two groups let alone energy for all the other predators of zooplankton. Steele (1974) used a yearly P/B ratio for zooplankton of 7 for his calculations for the North Sea, which

may be conservative for the shelf and slope water considering the energy requirements of the euphausiids and myctophids. To estimate the approximate annual production of zooplankton in the shelf water, a P/B of 7 was multiplied by the mean of the April and June biomass values to give a value of 1103 $kJ \cdot m^{-2} \cdot yr^{-1}$. Assuming the energy requirements of the myctophids and euphausiids were similar for the entire year to those measured in April and June, they would consume about 365 kJ per year or about 33% of the copepod production per year. This value is only a rough approximation because the real P/B for zooplankton is not known.

The biomass of chaetognaths was low (≈ 1 g/m^2) during all three sample periods. A rough estimate of the production of chaetognaths and their consumption of zooplankton can be made if it is assumed that their turnover rate is similar to *Sagitta elegans* found inshore, which was estimated at 2.0 (Sameoto 1971), and that their transfer efficiency was 32% (Reeve 1968). The dry weight of chaetognaths was 8.3% of the wet weight (Sameoto 1971) and the number of kilojoules per gram dry weight was 19.7 (Sameoto 1971). Using these values it was estimated from the April 1979 data which gave a mean biomass of about 1 g wet weight/m^2 that the yearly production of chaetognaths in the shelf water on the slope was 3 kJ and that their consumption of zooplankton and microzooplankton was 9.6 kJ, because the biomass of chaetognaths in inshore water reaches its maximum in March and April (Sameoto 1971). By using the maximum biomass values, the production and consumption may be overestimated rather than underestimated. Therefore these results do not support the hypothesis suggested by Mills and Fournier (1980) that a food chain dominated by chaetognaths utilizing microzooplankton exists in the shelf and slope waters at least during the spring period.

Gelatinous carnivores such as ctenophores and medusae were in good shape when collected with the BIONESS which meant that few if any were damaged and lost through the mesh of the nets. Therefore, the values given for the abundance of these animals can be considered to be close to the actual numbers in the two water masses sampled. During all three sampling periods the numbers of cnidaria $\cdot m^{-2}$ were very low, as a result the suggestion made by Mills and Fournier (1979) that these animals may be a possible dominant predator in the region of the shelf–slope front was not supported by this study.

The data on urochordate numbers did support the statement by Mills and Fournier (1979) that this group of animals can be very abundant in the shelf–slope front region, and they suggested that pelagic tunicates, when abundant, can play an important role in transferring organic matter to the benthos through the fecal material. In this study the salps were abundant on one station in 1979 suggesting a very patchy distribution in the shelf water. They were not abundant in the slope water during any year.

The acoustic echograms showed that the intensity of backscattering in the upper 100 m during the night was relatively uniform for many kilometres in the shelf water, but that an abrupt decrease in the intensity occurred at the front of the shelf and slope water that followed the temperature contours less than 12°C. As the water became warmer the amount of acoustic scattering decreased. The data from the BIONESS samples in the shelf and slope water and results of Sameoto and Lewis (1980a, b) showed that the most likely cause for the reduced scattering in the slope water was the marked reduction in the numbers of *C. finmarchicus*, euphausiid adults, and adult *B. glaciale*. The reason for the reduction in these animals can only be surmized, but it does not appear to be related to the amount of chlorophyll *a* which was actually higher in the warmer slope water south of the shelf–slope front (Herman et al. 1981). The acoustic data from May 1977 and April 1979 suggested that the distribution of animals was related either directly or indirectly to the temperature.

The shelf–slope frontal region is very dynamic and its position relative to the shelf break can vary year to year as was shown in this study and by Smith et al. (1978). The position of the front probably has profound effects on the abundance of zooplankton and micronekton in the area which in turn may be reflected at a later time in the fishery of the region, a point recognized by Mills and Fournier (1979) when they discussed the importance of this region to the pelagic fishery of the Nova Scotian slope.

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NOTES

A Rapid High-Performance Liquid-Chromatographic Method for Simultaneously Determining the Concentrations of TFM and Bayer 73 in Water During Lampricide Treatments

V. K. DAWSON

U.S. Fish and Wildlife Service, P.O. Box 818, La Crosse, Wisconsin 54601, USA

DAWSON, V. K. 1982. A rapid high-performance liquid-chromatographic method for simultaneously determining the concentrations of TFM and Bayer 73 in water during lampricide treatments. Can. J. Fish. Aquat. Sci. 39: 778 – 782.

The high-performance liquid-chromatography (HPLC) procedure requires only minutes per sample, is specific, and is relatively sensitive (limit of detection <0.005 mg/L for both chemicals). A combined buffer (pH 4) and internal standard (3-chlorodiphenylamine) reagent is added to the water sample, which is injected through a Sep Pak C_{18} disposable cartridge. The cartridge adsorbs and retains both the lampricides and the internal standard. The quantitative elution of the three chemicals from the cartridge with a small volume of methanol effectively concentrates the sample and provides sample cleanup. The methanol extract is then analyzed directly by HPLC on an MCH 10 reverse phase column by using a methanol:0.01 mol/L acetate buffer (87:13, v:v) as the mobile phase at 2 mL/min and detected by ultraviolet spectrophotometry at 330 (or 254) nm. A microprocessor data system further facilitates the procedure by quantifying off-scale peaks and yielding results directly in units of concentration (mg/L).

Key words: sea lamprey, lampricides, methodology, chromatographic techniques, 3-trifluoromethyl-4-nitrophenol, 2′,5-dichloro-4′-nitrosalicylanilide, streams

DAWSON, V. K. 1982. A rapid high-performance liquid-chromatographic method for simultaneously determining the concentrations of TFM and Bayer 73 in water during lampricide treatments. Can. J. Fish. Aquat. Sci. 39: 778 – 782.

La chromatographie en phase liquide à haute performance (HPLC) ne requiert que quelques minutes par échantillon, est spécifique et relativement sensible (limite de détection <0,005 mg/L pour les deux substances chimiques). On ajoute à l'échantillon d'eau une combinaison d'un tampon (pH 4) et d'un réactif interne standard (3-chlorodiphénylamine), qui est injectée à l'aide d'une cartouche rejetable Sep Pak C_{18}. La cartouche absorbe et retient à la fois les lampricides et le réactif standard. L'élution quantitative des trois substances chimiques de la cartouche avec un petit volume de méthanol concentre effectivement l'échantillon et en assure le nettoyage. L'extrait de méthanol est ensuite analysé directement par HPLC sur colonne en phase inversée MCH 10 en utilisant un tampon méthanol:acétate 0,01 mol/L (87:13, v:v) comme phase mobile à 2 mL/min, et détecté par spectrophotométrie à l'ultraviolet à 330 (ou 254) nm. Un système de traitement de l'information par micro-ordinateur facilite les opérations en quantifiant les pics hors-échelles et donnant les résultats directement en unités de concentration (mg/L).

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THE application of chemical lampricides has been successfully used for control of the parasitic sea lamprey (*Petromyzon marinus*) in the Great Lakes. Applegate et al. (1958) reported that 3-trifluoromethyl-4-nitrophenol (TFM) was selective against the sea lamprey. The addition of small amounts of the ethanolamine salt of 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) to TFM greatly reduced the amount of TFM required for effective control of lamprey populations (Howell et al. 1964). Because Bayer 73 is also toxic to other fishes and is virtually nonselective for lampreys over rainbow trout (*Salmo gairdneri*), no more than 3% by weight may be added to TFM without reducing the selective toxicity of TFM (Howell et al. 1964). Since 1963, mixtures of TFM and

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Bayer 73 have been used to control lampreys in tributaries of the Great Lakes by both the United States and Canadian governments (Hamilton 1974).

Use of the mixture has produced occasional fish kills that could not be predicted on the basis of pretreatment toxicity tests (U.S. Bureau of Commercial Fisheries 1968). These fish kills have been variously attributed to problems with formulation, application, water chemistries, or a combination of these factors (U.S. Bureau of Commercial Fisheries 1964, 1968; Smith 1966). Some of the problems related to application rates could be corrected by the use of rapid, accurate analyses to monitor concentrations of the lampricides during chemical treatments. A rapid colorimetric procedure is currently used to monitor TFM concentrations (Smith et al. 1960). Several methods have been reported for the analysis of Bayer 73 in water using colorimetry (Strufe 1962; Daniels et al. 1965; El-Dib and Aly 1972; Dawson et al. 1978); however, their utility for monitoring treatment concentrations is limited by problems with sensitivity, interferences, or analysis time. Gas–liquid chromatography methods have been proposed for the analysis of TFM (Allen and Sills 1974; Coburn and Chau 1976) and Bayer 73 (Luhning et al. 1979; Muir and Grift 1980; Abidi 1979). However, all of these methods require the use of hydrolysis or derivitization, both of which are time consuming. Muir and Grift (1980) reported the analysis of niclosamide (Bayer 73) in water and sediment by using high-performance liquid chromatography (HPLC) on an NH_2-Bondapak column.

The objective of the present study was to determine if HPLC could be adapted into a rapid, specific, and sensitive method for the simultaneous determination of TFM and Bayer 73 concentrations in water during lampricide treatments.

Materials and methods — The procedure involves sample concentration on a disposable adsorption column and subsequent separation and quantification using HPLC with UV detection. The required equipment and reagents needed and stepwise procedure follow.

Apparatus

1. HPLC, Varian 5000 equipped with varichrom UV detector and optional CDS-111L data system. Operating conditions: stationary phase, 30 cm × 4 mm Varian micropak MCH 10 reverse phase; mobile phase, methanol:0.01 mol/L acetate buffer (87:13, v:v); flow rate, 2 mL/min; chart speed, 1 cm/min; wavelength, 330 or 254 nm; attenuation, 0.04 absorbance full scale.
2. Sep Pak® C_{18} disposable cartridges from Waters Assoc. Inc.
3. Vortex stirrer.
4. Disposable syringes (30 or 50 mL).
5. Test tubes (15 mL) with Teflon-lined screw caps.

Reagents

1. Methanol, HPLC grade from J. T. Baker Inc.
2. Water, HPLC grade from J. T. Baker Inc.
3. TFM, purified grade from Aldrich Chemical Co., 0.01 g/100 mL methanol.
4. Bayer 73, technical grade from Chemagro Corp., 0.01 g/200 mL methanol (made fresh weekly).
5. 3-Chlorodiphenylamine (CDPA), ACS reagent grade from Aldrich Chemical Co., stock A: 1 mL/100 mL methanol, stock B: 1 mL stock A/100 mL methanol.
6. Acetic acid (glacial), ACS reagent grade from Fisher Scientific Co., 0.2 mol/L: 11.6 mL diluted to 1 L with water.
7. Sodium acetate, ACS reagent grade from Fisher Scientific Co., 0.2 mol/L: 2.72 g of $C_2H_3O_2Na \cdot 3H_2O$ diluted to 100 mL with water.
8. Buffer (0.01 mol/L) for mobile phase. 41 mL 0.2 mol/L acetic acid + 9 mL 0.2 mol/L sodium acetate diluted to 1 L with water.
9. Buffer/CDPA reagent (0.1 mol/L) 41 mL 0.2 mol/L acetic acid + 9 mL 0.2 mol/L sodium acetate + 7.5 mL CDPA (stock B) diluted to 100 mL with water.
10. Stock solution of procedure standards (1 mg/L TFM and 0.1 mg/L Bayer 73), 1 mL TFM + 0.2 mL Bayer 73 diluted to 100 mL with water.

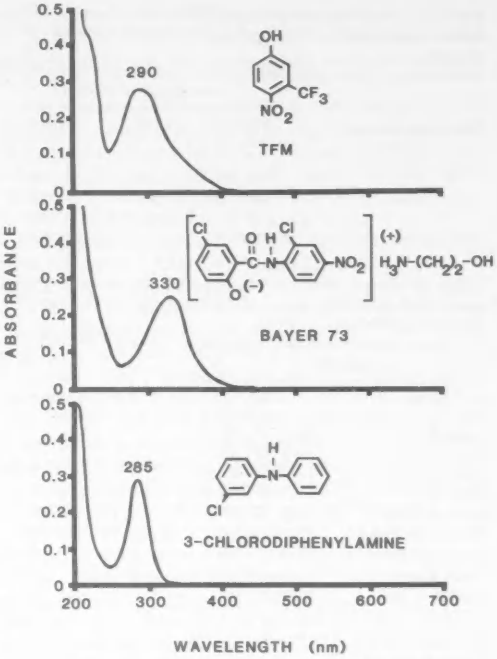

FIG. 1. Chemical structures and UV spectra of TFM (10 mg/L), Bayer 73 (5 mg/L), and 3-chlorodiphenylamine (2.5 mg/L) in methanol:0.01 mol/L acetate buffer (87:13, v:v).

Procedure

1. Precondition Sep Paks with 2 mL methanol and 5 mL water according to instruction sheet supplied by manufacturer.
2. Add 2 mL buffer/CDPA internal standard to 30-mL water sample.
3. Attach preconditioned Sep Pak to 30-mL syringe with plunger removed.
4. Transfer sample to syringe, insert plunger, and force sample through Sep Pak at not more than 40 mL/min.

TABLE 1. Percentage of recovery of TFM, Bayer 73, and 3-chlorodiphenylamine (CDPA) from Sep Paks with selected methanol elution volumes.

Elution volume (mL)	Percentage of recovery		
	TFM	CDPA	Bayer 73
0.5	7.1	<1	<1
1.0	91.5	88.4	45.2
1.5	100	100	95.6
2.0	99.5	96.7	100

TABLE 2. Site of collection, pH, and alkalinity of water samples treated with lampricide and used for determination of lampricide recoveries (Table 3).

Sample		pH	Alkalinity as $CaCO_3$ (mg/L)
Source	Site		
Cedar River	Hwy. 35, MI	—	—
Dexter Creek	Hwy. 67, MI	7.5	97
Chocolay River	Co. Rd. 480, MI	7.1	53
Sand River	Co. Rd. 480, MI	4.5	—
Johnson Creek	Hwy. 67, MI	7.3	68
Mississippi River	Hwy. 16, WI	9.0	181
La Crosse River	Hwy. 35, WI	9.0	142
Black River	Lytles, WI	8.1	242
Halfway Creek	Midway, WI	8.4	249

Discard water.

5. Remove Sep Pak, remove plunger, and then replace Sep Pak on syringe.

6. Add 1.5 mL methanol, insert plunger, and slowly force methanol through Sep Pak into test tube.

7. Cap tube and mix.

8. Analyze by HPLC against 30 mL of a standard containing known concentrations of TFM and Bayer 73 in water solution carried through the Sep Pak concentrating procedure above.

Results and discussion — Because its adsorptive characteristics on Sep Pak cartridges were similar to those of the lampricides, CDPA was selected as an internal standard. Its liquid chromatogram gives good baseline separation with a mobile phase that provides short retention times for all components without gradient programming. Short retention times are vital for the development of a rapid analytical procedure.

The chemical structures and UV spectra of TFM, Bayer 73, and CDPA are presented in Fig. 1. Because the concentration of Bayer 73 used in lampricide treatments is considerably less than that of TFM, one of the considerations for the selection of wavelength for UV detection was optimization of the detection of Bayer 73 (330 nm). Because economics must often be considered in equipping a mobile laboratory, the wavelength of less-expensive monochromatic detectors (254 nm) was also evaluated. A wavelength of 254 nm provided good results, but the sensitivity for the detection of Bayer 73 was only about half that at 330 nm.

Because both TFM and Bayer 73 are phenols and have ionizable hydroxyl groups, an acetate buffer (0.01 mol/L) at pH 4.0 was used as part of the carrier solvent for ion suppression. Muir and Grift (1980), using a methanol:water solvent system on NH_2-Bondapak columns, noted changes in the retention time of niclosamide (Bayer 73 without the ethanolamine salt) during a normal operating day. They reduced the variation by continuously sparging the solvent with helium. Use of the 0.01 mol/L acetate buffer for pH regulation and ion suppression stabilized retention times in the present study.

The rate of flow of water samples through the Sep Paks during extraction, and the elution rate of methanol, affect recoveries. The recovery of each chemical was only about 70%, at a flow of 100 mL/min, but exceeded 95% at flows of 40 mL/min or less. Because the adsorptive characteristics of the internal standard are very similar to those of the lampricides, recoveries of all three components drop at about the same rate even if optimum flow rates are exceeded. Most experimental error is corrected by using internal standard quantification.

TABLE 3. Percentage of recovery of TFM (1 mg/L), Bayer 73 (0.1 mg/L), and CDPA (1 mg/L) from treated water samples by Sep Pak extraction and HPLC analysis.

Sample	Percentage of recovery					
	TFM		CDPA		Bayer 73	
	U[a]	B[b]	U	B	U	B
Cedar River	62.8	90.7	88.2	93.1	76.7	94.9
Dexter Creek	64.4	94.9	89.7	92.8	83.7	92.0
Chocolay River	70.2	87.3	91.6	81.8	79.8	89.7
Sand River	108	98.3	84.9	83.8	87.7	94.3
Johnson Creek	65.9	125	81.8	90.5	107	91.3
Mississippi River	67.7	100	91.4	87.0	102	84.0
La Crosse River	119	100	82.9	82.0	100	97.0
Black River	76.8	100	79.7	79.0	97.5	89.0
Halfway Creek	62.7	100	83.0	83.0	91.8	86.0
HPLC grade water	59.3	95.4	81.3	80.4	90.7	99.8
Mean	75.7	99.2	85.5	85.3	91.7	91.8
SE	6.5	3.2	1.4	1.6	3.1	1.5

[a]U = unbuffered.

[b]B = buffered to pH 4.0 with acetate buffer.

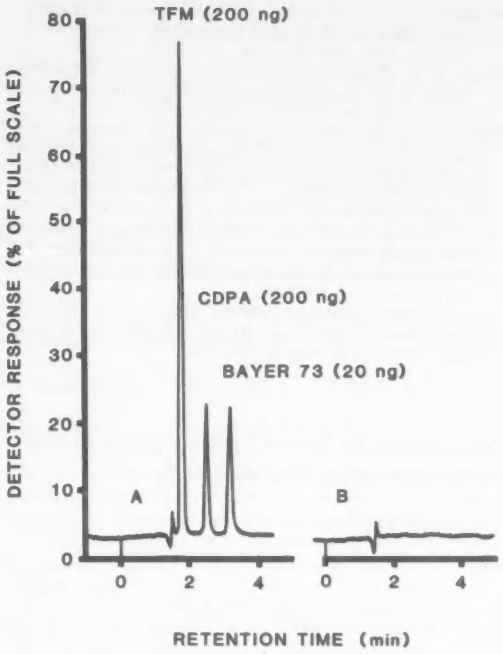

FIG. 2. Liquid chromatography of (A) Cedar River water sample treated with TFM (1.0 mg/L), CDPA (1.0 mg/L), and Bayer 73 (0.1 mg/L) and (B) untreated Cedar River water using a mobile phase of methanol:0.01 mol/L acetate buffer (87:13, v:v) at 2 mL/min, 330 nm, and 0.04 AFS. Water sample (30 mL) concentrated 20× on Sep Pak by eluting with 1.5 mL methanol.

Several volumes of methanol were evaluated for extraction of adsorbed chemicals from Sep Paks (Table 1). Small volumes of methanol provide greater sample concentration, but recoveries were poor if less than 1.5 mL of methanol was used for elution.

As indicated in step 1 of the procedure, the Sep Paks must be prerinsed with methanol followed by water before they are used in the analyses. For best results, this step should not be completed more than 2 h before an analysis.

For convenience, the buffer and internal standard are combined in one reagent (step 2 of the procedure). The internal standard (CDPA) was stable in the buffer for more than 2 wk at room temperature.

Dawson et al. (1978) noted significant interferences in the colorimetric analysis of Bayer 73 in certain natural waters, particularly those with high concentrations of tannins and lignins. To evaluate possible interferences, water samples from nine streams (Table 2) were treated with lampricides and then analyzed. One of the samples was collected from Cedar River, a river in which Dawson et al. (1978) had observed interferences. Some water samples exhibited poor recoveries of TFM, presumably because the molecule was ionized at alkaline pH's. When the pH of the same samples was adjusted to 4.0 before adsorption on Sep Paks, recoveries were good with no apparent interferences (Table 3). Recoveries from treated, unbuffered water samples averaged 75.7, 85.5, and 91.7% for TFM, CDPA, and Bayer 73, respectively. When buffered to pH 4.0, the corresponding recoveries averaged 99.2, 85.3, and 91.8%.

A typical liquid chromatogram of water samples spiked with TFM (1 mg/L), CDPA (1 mg/L), and Bayer 73 (0.1 mg/L) is presented in Fig. 2. The retention times with a solvent system of methanol:0.01 mol/L acetate buffer (87:13, v:v) flowing at 2 mL/min were 1.8, 2.5, and 3.2 min for TFM, CDPA, and Bayer 73, respectively.

Five replicate samples of Sand River water treated with TFM (2.5 mg/L), CDPA (0.5 mg/L), and Bayer 73 (0.05 mg/L) were analyzed to evaluate the consistency of the method. Mean percentages of recovery and standard errors (in parentheses) were as follows: TFM, 92.9 (2.1); CDPA, 97.8 (1.3); and Bayer 73, 90.8 (3.2).

A water-sample volume of 30 mL is sufficient if anticipated lampricide concentrations are near 0.02 mg/L. However, 150–200 mL of water may be required to achieve a sensitivity of 0.005 mg/L. The limiting factors for greater sample concentration are the tedium of extracting large volumes of sample and possible interferences that may develop in samples as a result of contaminant extraction and concentration.

Because TFM is applied at much higher concentrations than Bayer 73, concentration steps required for detection of Bayer 73 may cause TFM chromatograms to go off-scale. These peaks can still be quantified through the use of a microprocessor data system such as a Varian CDS-111L. This system is linear beyond 300 mg/L of TFM and is capable of converting peak areas to concentration units. If a data system is not available, samples having peaks extending off-scale must be diluted and reinjected.

Bayer 73 undergoes hydrolysis under certain conditions to form 2-chloro-4-nitroaniline and 5-chlorosalicylic acid (Luhning et al. 1979). However, these breakdown products have different retention times than TFM, Bayer 73, or CDPA on HPLC and therefore do not interfere with the HPLC analysis.

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Corrected Analysis of the Ability to Detect Reductions in Year-Class Strength of the Hudson River White Perch (*Morone americana*) Population[1,2]

DOUGLAS S. VAUGHAN AND WEBSTER VAN WINKLE

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830, USA

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This analysis presents a correction of that presented in Van Winkle et al. (1981; Can. J. Fish. Aquat. Sci. 38: 627–632). An exact solution is obtained based on the noncentral *t*-distribution to replace the incorrect solution based on the central *t*-distribution used in our earlier analysis. Our new results, although less pessimistic than before, still are not encouraging. They indicate that variability in baseline data is so great that data from 10 additional years are not adequate for detecting even substantial (>50%) reductions in mean year-class strength, and that at least 20 years of data collection would be required to detect an actual 50% reduction in mean year-class strength, given a Type II error of 50%.

Key words: fractional reduction, impingement, power plant, statistical power, Type I and Type II errors, white perch, year-class strength

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L'analyse décrite dans le présent article corrige celle présentée par Van Winkle et al. (1981; Can. J. Fish. Aquat. Sci. 38: 627–632). On arrive à une solution exacte fondée sur une distribution non centrale de *t* plutôt que sur une fondée sur la distribution centrale de *t* incorrectement utilisée dans notre analyse précédente. Bien que moins pessimistes qu'avant, ces nouveaux résultats ne sont quand même pas encourageants. Ils démontrent que la variabilité des données de base est si grande que 10 années supplémentaires de données ne suffiraient pas à détecter même des diminutions substantielles (>50%) d'abondance

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moyenne des classes d'âge et qu'il faudrait accumuler des données pendant au moins 20 ans pour détecter une diminution réelle de 50 %, avec erreur de Type II de 50 %.

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In this note a correction is presented to a method described in Van Winkle et al. (1981) for detecting reductions in mean year-class strength of the young-of-the-year white perch (*Morone americana*) population in the Hudson River. We present here an exact solution based on the noncentral *t*-distribution, to replace what amounts to an incorrect solution based on the central *t*-distribution used in our prior analysis.

Noncentral t-distribution — The noncentral *t*-distribution is given by the ratio (Johnson and Kotz 1970):

$$(1)\quad t'_\nu(\delta) = (U + \delta)/(\chi_\nu/\sqrt{\nu}),$$

where U and χ_ν are independent random variables distributed as standard normal $[N(0,1)]$ and chi (as in chi-square) with ν degrees of freedom, respectively, and δ is the noncentrality parameter. The integral of (1) from minus infinity to some real number, t^*, is evaluated by a function subroutine (MDTN) available from IMSL (1975). To obtain the probability that the random variable $t'_\nu(\delta)$ is less than or equal to the real number, i.e.

$$(2)\quad \Pr\{t'_\nu(\delta) < t^*\}$$

the values for t^*, δ, and ν are required.

To test the null hypothesis H_0: $\mu_1 = \mu_2$ against the alternative hypothesis H_A: $\mu_1 > \mu_2$, the appropriate test statistic [Van Winkle et al. (1981); Eq. (3)] is given by

$$(3)\quad t' = \frac{\overline{X}_1 - \overline{X}_2}{\sqrt{s_p^2\,(1/n_1 + 1/n_2)}},$$

where

$$(4)\quad s_p^2 = \frac{(n_1 - 1)\,s_1^2 + (n_2 - 1)\,s_2^2}{n_1 + n_2 - 2}.$$

The sample means $\overline{X}_1$ and $\overline{X}_2$ are from two randomly drawn, independent samples of indices of year-class strength, s_1^2 and s_2^2 are sample variances, and n_1 and n_2 are sample sizes (i.e. number of years).

As described in Van Winkle et al. (1981, Eq. (5)), under the null hypothesis (H_0: $\mu_1 - \mu_2 = 0$)

$$(5)\quad \Pr\{t > t_{\nu,\alpha}\} = \alpha,$$

where t has a central *t*-distribution and α is the Type I error, or probability of rejecting the null hypothesis when true. The alternative hypothesis (H_A: $\mu_1 - \mu_2 > 0$) implies that

$$(6)\quad \Pr\{t > t_{\nu,\alpha}\} = 1 - \beta,$$

where t now has a noncentral *t*-distribution with noncentrality parameter (Johnson and Kotz 1970):

$$(7)\quad \delta = (\mu_1 - \mu_2)\Big/\sqrt{\sigma^2\,(1/n_1 + 1/n_2)},$$

and β is the Type II error, or probability of accepting the null hypothesis when it is false. The power of a statistical test $(1 - \beta)$ is the probability of correctly rejecting the null hypothesis.

The statement "the difference on the left side of the inequality in (7) is distributed under H_A as a central *t*-distribution" following (7) in Van Winkle et al. (1981) is incorrect. Subtracting the noncentrality parameter from both sides of (6) does not transform the noncentral *t*-distribution to the central *t*-distribution. The results that follow in this paper are based directly on evaluating the noncentral *t*-distribution through its noncentrality parameter, δ.

Results — If the first sample has already been obtained, then n_1 and estimates of μ_1 and σ^2 are available ($\overline{X}_1$ and s_1^2, respectively). Replacing s_p^2 and reducing the degrees of freedom to $\nu = n_1 - 1$ (Baker 1935) in (3), then (6) can be evaluated by first substituting into (7) $b\overline{X}_1 = \overline{X}_1 - \overline{X}_2$ for $\mu_1 - \mu_2$ where b is the fractional reduction in mean year-class strength, and s_1^2 for σ^2, so that

$$(8)\quad \sigma = b/\mathrm{CV}\,\sqrt{1/n_1 + 1/n_2},$$

where $\mathrm{CV} = s_1/\overline{X}_1$ is the coefficient of variation. Figures 1 and 2 presented in this note are analogous to Fig. 1 and 2 in Van Winkle et al. (1981) where n_1 is set equal to 5; note that the legends for Fig. 1 and 2 have been reversed. For a given sample size, n_2, and fractional reduction in year-class strength, b, the statistical power is now higher than previously reported. This implies that either a smaller sample size, n_2, will suffice, or a lower fractional reduction in year-class strength can be detected for a specified level of statistical power. The sample sizes, n_2, indicated on Fig. 1 and the fractional reductions in year-class strength, b, indicated on Fig. 2 are less than we previously reported.

Analogous to (16) in Van Winkle et al. (1981), allowing n_2 to approach infinity in (7) implies that the minimum detectable fractional reduction in mean year-class strength, b, approaches a lower bound, B, which is obtained from the relation

$$(9)\quad \delta = B/\mathrm{CV}\,\sqrt{1/n_1}.$$

Because this equation cannot be used directly to obtain values of B, the absolute minimum detectable fractional reduction in mean year-class strength for different levels of power, Fig. (3) was developed. Specifying the preimpact sample size, n_1, the coefficient of variation, CV, and a desired level of statistical power, $1 - \beta$, Fig. (3) allows one to estimate B. For statistical power equal to 0.5, the absolute minimum

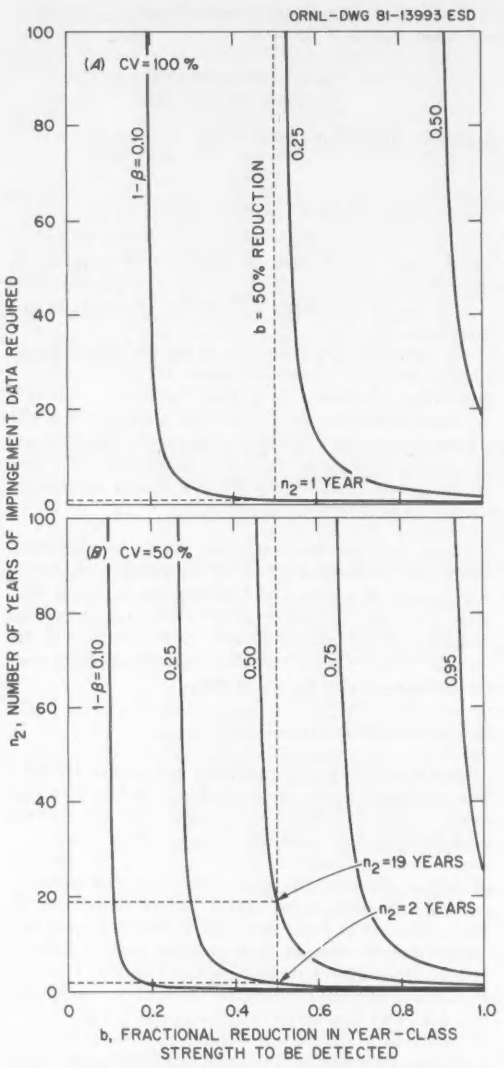

FIG. 1. Number of years of additional impingement data (starting in 1978) required to detect a specified fractional reduction in mean year-class strength of young-of-the-year white perch in the Hudson River. Curves are drawn for $\alpha = 0.05$ over a range of powers $(1 - \beta)$, for $n_1 = 5$ years of pre-1978 data and for two values of the coefficient of variation (CV): (A) CV = 100% and (B) CV = 50%. Values of n_2 on the figure are the number of additional years of data required, for the specified statistical powers, to detect a 50% reduction in mean year-class strength.

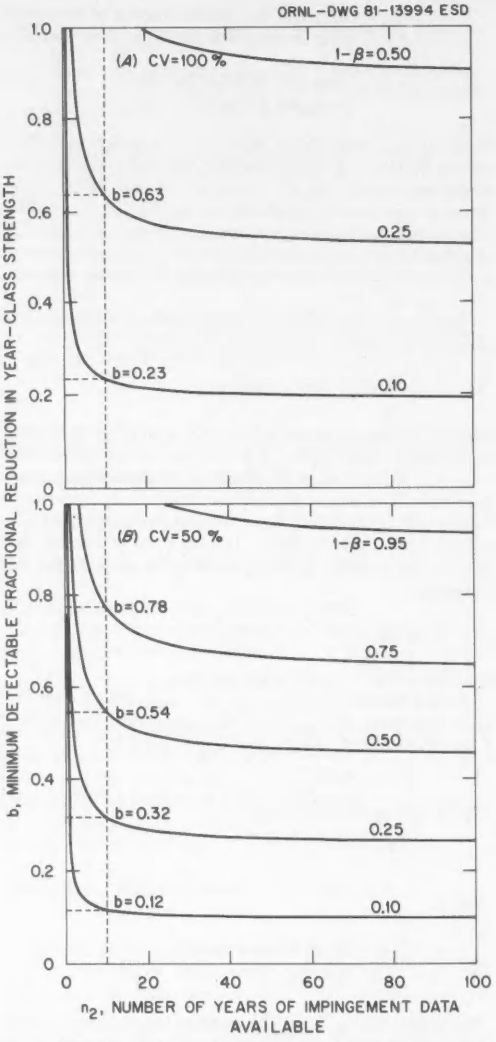

FIG. 2. Fractional reduction in mean year-class strength of young-of-the-year white perch in the Hudson River as a function of the number of additional years for which impingement data are available (starting in 1978). Curves are drawn for $\alpha = 0.05$ over a range of powers $(1 - \beta)$, for $n_1 = 5$ years of pre-1978 data and for two values of the coefficient of variation (CV): (A) CV = 100% and (B) CV = 50%. Values of b on the figure are the minimum fractional reductions that could be detected for the specified statistical powers, to detect a 50% reduction in mean year-class strength.

detectable fractional reduction in year-class strength is 0.44 for CV = 50% and is 0.88 for CV = 100%.

Discussion — Results presented here can differ appreciably from those presented in our earlier report, where the central t-distribution was incorrectly used in place of the noncentral t-distribution. Our results are still not encouraging to the researcher or manager needing to employ this overall approach, although they are not as pessimistic as previously

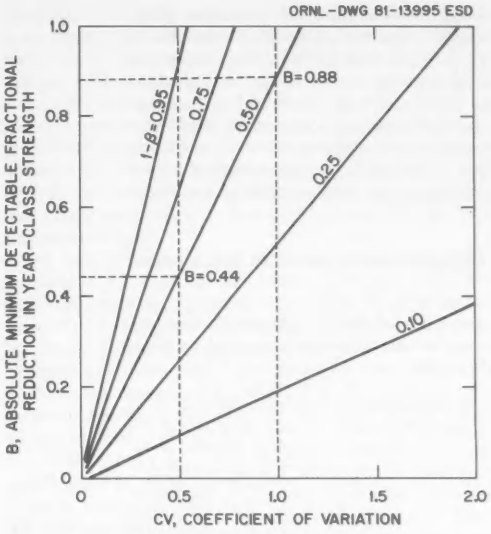

FIG. 3. Absolute minimum fractional reduction (B) in mean year-class strength of young-of-the-year white perch in the Hudson River as a function of the coefficient of variation (CV). Curves are drawn for $\alpha = 0.05$ over a range of powers ($1 - \beta$), and for $n_1 = 5$ years of pre-1978 data. Values of B on the figure are the minimum fractional reductions that could be detected for the specified statistical powers given an infinite number of years of additional data.

reported (Van Winkle et al. 1981). Variability in the baseline time series of impingement data is such that for CV = 50%: (a) approximately half the expected lifetime of the power plants involved (typically 40 years of power plant operation) of additional data would be required to detect an immediate 50% reduction in the mean index of year-class strength, even if one is willing to accept a Type II error (β) as large as 50% (Fig. 1B); and (b) 10 additional years of indices of year-class strength still are not likely to detect a substantial reduction ($b = 50\%$) in mean year-class strength for even a minimal level of power (Fig. 2B). With a coefficient of variation (CV) on the order of 100%, even an infinite number of additional indices of year-class strength is insufficient for determining a fractional reduction in mean year-class strength of 50% with a Type II error as large as 75% (or power as small as 25%) (Fig. 1A and 3).

Bearing in mind the caveats discussed in Van Winkle et al. (1981), the methodology presented here is applicable whenever a time series of indices of year-class strength is available. Therefore, we continue to argue that fluctuations in year-class strength (for which the Hudson River white perch is typical) can mask major reductions in mean year-class strength. Thus our approach provides a generic tool for establishing bounds on the minimum detectable reduction in fish stocks and on the number of additional years of data needed to detect a specified reduction.

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A Comparison of Different Phosphorus Fractions as Predictors of Particulate Pigment Levels in Lake Memphremagog and its Tributaries

ROBERT HENRY PETERS

Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Que. H3A 1B1

AND MARTIN BERGMANN

Department of Zoology, University of Manitoba, Winnipeg, Man.

PETERS, R. H., AND M. BERGMANN. 1982. A comparison of different phosphorus fractions as predictors of particulate pigment levels in Lake Memphremagog and its tributaries. Can. J. Fish. Aquat. Sci. 39: 785–790.

The amounts of colored particulate material (measured by reflectance) in surface waters of Lake Memphremagog and its tributaries were regressed against concentrations of total

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phosphorus and several of its component fractions: soluble phosphorus, particulate phosphorus, soluble reactive phosphorus, orthophosphate, large molecular weight phosphorus (>5000 mol wt) and small molecular weight phosphorus (<400 mol wt). The correlations were examined to see if one of these fractions was a better predictor of seston concentration, and presumably of other biologically related lake properties, than total P, and to determine if riverine samples differed from lake waters in the relation between concentrations of P and suspended particulates. Total P correlated with colored particulates in both lotic and lentic samples as well as or better than any other fraction. Although river samples showed greater variation than lake samples, the regression lines describing the relations were similar in both lakes and rivers.

Key words: phosphorus fractions, lakes, rivers, empirical models, particulate concentration, seston

PETERS, R. H., AND M. BERGMANN. 1982. A comparison of different phosphorus fractions as predictors of particulate pigment levels in Lake Memphremagog and its tributaries. Can. J. Fish. Aquat. Sci. 39: 785–790.

Nous avons calculé le régression de la quantité de matériel particulaire colorée (mesurée par reflectance) dans les eaux de surface du lac Memphremagog et ses tributaires sur les concentrations de phosphore total et plusieurs de ses composants : phosphore soluble, phosphore particulaire, phosphore réactif soluble, orthophosphate, phosphore à poids moléculaire élevé (> 5 000 p.m.) et phosphore à faible poids moléculaire (< 400 p.m.). Ces corrélations ont été examinées afin de déterminer si l'une de ces fractions était préférable au P total comme indice de concentration du seston et probablement d'autres propriétés biologiquement reliées des lacs. On voulait également déterminer si la relation entre les concentrations de P et celles de particules en suspension différait entre les échantillons de rivières et ceux des lacs. Il y a aussi bonne, sinon meilleure relation entre le P total et le matériel particulaire coloré, tant dans les échantillons lotiques que lentiques, que dans toute autre fraction. Bien que la variation soit plus grande dans les échantillons de rivières que dans ceux de lacs, les droites de régression décrivant les relations sont identiques.

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THE concentration of total phosphorus is well established as a predictor of many biologically mediated lake properties (Cornett and Rigler 1979; Nicolls and Dillon 1978). However, the large residual variation in these empirical relationships shows that other factors must be considered to improve our predictive and managerial understanding of lakes. Several authors (Schaffner and Oglesby 1978; Peters 1979, 1981; Williams et al. 1980) have suggested that total phosphorus analyses include forms of phosphorus which are not biologically available. If this is so, some component of total P concentration should yield improved predictions of biologically mediated lake properties. Although no such index of biologically active P has been demonstrated, it would be a simple procedure to compare the correlation between different P fractions and some other lake characteristic and so to determine which of several fractions yields the best regression.

This paper investigates the possibility that the concentration of one of the more commonly measured P fractions (orthophosphate, soluble reactive P, soluble P, and particulate P) or of one of two soluble fractions identified by gel filtration analysis (large molecular weight P, >5000 mol wt, or small molecular weight P, <400 mol wt) is a better predictor of sestonic pigment than is total P concentration. We have previously shown that sestonic pigment is correlated with both total P and chlorophyll concentration and, to a lesser degree, with seston mass (Bergmann and Peters 1980). In this study, pigment level is therefore considered a representative of that suite of lake properties which have been related to total P. Its choice was dictated by practical limitations: P fractions were analyzed as part of a previously published study (Peters 1979) of the P cycle in lake Memphremagog, and sestonic pigment was the only simultaneous index of biological development in the lake which could be obtained post facto.

Lake Memphremagog is a suitable site for such a study because that lake shows a marked axial gradient in P concentration (Peters 1979). The south-to-north decline in P concentration correlates with similar decreases in biomass and production of phytoplankton (Ross and Kalff 1975), benthos (Dermott et al. 1977), and fish (Gascon and Leggett 1977; Nakashima and Leggett 1975). These trends plus changes in phytoplankton structure (Watson and Kalff 1981) and zooplankton biomass (McCauley and Kalff 1981) are similar to those obtained by comparisons among lakes of different trophic status. In short, in Lake Memphremagog the nutrient gradient follows the changes in biological responses that are more commonly depicted in regressions from many lakes; thus, a considerable range in both seston and P levels can be measured within a single water body, and these variations should represent those seen in a larger sample of lakes. One might suspect a priori that particulate P would be most closely associated with sestonic pigment; however, P is rapidly leached from freshly killed plankton (Cooper 1935;

Golterman 1964; Krause 1969; Peters 1981), and living particles account for only a small fraction of the total particulate carbon in aquatic systems (Hohl and Vagenknecht 1979; Reiswig 1972; Wetzel 1975); therefore, the relation of particulate color (a measure of all seston) with particulate P (a potential measure of plankton) need not be particularly close. In addition, some soluble P fractions are in a dynamic equilibrium with the plankton (Lean 1973), and these, or the sum of both particulate P and soluble fractions, may provide a more convenient index of biologically active P than does particulate P alone.

The Lake Memphremagog study also included the measurement of P fractions in lake tributaries (Peters 1978). We therefore took this opportunity to examine the relation between P concentration and particulate pigment level in rivers. One might expect the relation to differ from that in lakes. Limnetic particulate pigment is almost certainly dominated by biological material with which P is closely associated. In rivers a substantial portion of the P may not be biologically associated (Schaffner and Oglesby 1978; Williams et al. 1980), and colored inorganic particles may contribute significantly to particulate pigments. However, similarities between lakes and rivers in the proportions of different P fractions and their kinetic interactions (Peters 1978, 1979) might equally lead one to expect similar pigment–phosphorus relations in lakes and rivers.

Materials and methods — Details of sample collection and analyses have already been published (Peters 1977, 1978, 1979). Subsurface samples from Lake Memphremagog and its tributaries were collected from June 1975 to September 1976. Phosphorus concentrations of these samples were analyzed, in duplicate, with the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1968) preceded, when necessary, by digestion under pressure with potassium persulfate (Menzel and Corwin 1965). Particulate phosphorus was removed by filtration of 250 mL of whole lake or river water through 47-mm 0.45-μm millipore filters. Subsamples of this filtrate were analyzed directly for soluble reactive P or, after digestion, for soluble P. Particulate phosphorus was determined as the difference between total and soluble P concentrations. Soluble P was also separated into two broad fractions, large molecular weight P and small molecular weight P, by passing other filtrate subsamples through gel filtration columns filled with G-25 fine Sephadex gel. Finally a radiobiological assay was used to determine orthophosphate concentrations (Peters 1977, 1978, 1979).

When natural waters are passed through Millipore filters, the filters are discolored in proportion to the amount of particulate material in the water (Vallentyne et al. 1970). We (Bergmann and Peters 1980) quantified this discoloration by photometric measurement of the reduction in the amount of defined light reflected from the surface of such filters (R_s) relative to that reflected from an unused filter (R_c) and that collected by the photometer when the incident light beam was turned off (R_d). An index of reflectance, R, was then defined as

$$R = [(R_s - R_d) \cdot 100]/(R_c - R_d).$$

We then showed that this index varied semilogarithmically with seston concentration, that it was a better correlate of chlorophyll concentration than total P in across-lake comparisons, and that it was little affected by prolonged storage of the filters.

Filters for the present analyses were those used to separate soluble from total P. These had been air-dried and glued into data books, originally as a simple visual record of seston concentration. During the winter of 1978–79, these were cut from the books and their reflectance measured. Unfortunately, many of the filters had become glued to facing pages and broke when we attempted to open the books. Fully 29% of all 189 filters were destroyed in this way. A further 14% of the samples lacked complete descriptions of the P fractions and were eliminated from analysis. Thus of the original 69 lake and 120 river samples, only 38 and 69, respectively, were used in the present study.

Our earlier work (Bergmann and Peters 1980) showed that 6 mo storage of filters resulted in a small loss of color and increase in variance. The present filters were stored for $3\frac{1}{2}$ yr, and this problem could have been aggravated. We tested for this in December 1981 by reanalyzing the reflectance of 23 filters which had been analyzed as part of our original cross-lake comparison. Reflectance of these filters were first measured within a month of collection in the summer of 1978 and again in January 1979. Reflectance values from each date were regressed against corresponding values from the same filters for earlier dates. If no changes had occurred the coefficient of determination (r^2) and the slopes in these regressions would be 1 and the intercept would be 0. The analyses (Table 1) showed that r^2 decreased with time (indicative of increasing variation), but neither the slopes nor intercepts were significantly affected. The average change in reflectance showed bleaching in filters stored for long periods, but this effect did not increase after 6 mo (Table 1). These results suggest that long storage alone would not seriously weaken the present treatment; they do not, however, address the possible effects of abrasion in the data books as the original set of 23 filters were not stored in books but in Glassine envelopes. The similarity of the regressions between reflectance and total phosphorus in this and the previous study (see Results and discussion) offers circumstantial evidence that abrasion was not pronounced.

The natural logarithm of reflectance (LnR) for lake or river samples was then regressed against each phosphorus fraction using a commercial statistical package (Barr et al. 1979) based on the method of least squares. This treatment can successfully distinguish the effects of the different fractions on reflectance if the concentrations of these components vary independently. Since all P fractions are, to some degree, dependent (Peters 1978, 1979; Rigler 1964), correlations were also derived between each pair of P fractions to demonstrate the degree of this interdependence.

It is also possible that LnR is predicted best by some complex function of these subfractions, for example, by particulate P minus large molecular weight P. To examine this possibility, stepwise multiple regression analyses of the data were performed. This treatment adds one new variable at each step until no further improvement ($P > 0.05$) can be made.

Results and discussion — In both Lake Memphremagog (Table 2) and its tributary streams (Table 3), sestonic pigment

TABLE 1. The effects of storage on reflectance from 23 samples of lake surface waters collected in July and August 1978 (Bergmann and Peters 1980). This table compares the degree of autocorrelation in reflectance measurements taken within a month of collection, then in January 1979 and again in December 1981.

Comparison x vs. y	R^2	Slope ± SE	Intercept ± SE	Mean change between analyses ± SE
1978 vs. 1979	0.90	0.91±0.066	1.50±5.1	−.08±0.95
1979 vs. 1981	0.81	1.11±0.12	−5.4±8.8	2.74±1.41
1978 vs. 1981	0.77	1.04±0.13	−5.42±9.4	−2.34±1.35

TABLE 2. Correlation matrix showing the coefficient of determinism (r^2) between a measure of seston concentration, the natural logarithm of reflectance (LnR), and seven phosphorus fractions: total P (TP), particulate P (PP), soluble P (SP), soluble reactive P (SRP), orthophosphate (PO_4), large molecular weight P (LMWP), and small molecular weight P (SMWP). Each correlation is based on 38 samples from lake Memphremagog, and hence there is a significant ($P < 0.05$) effect only when r^2 exceeds 0.093.

	TP	PP	SP	PO_4	SRP	SMWP	LMWP
LnR	0.469	0.402	0.367	0.110	0.155	0.043	0.055
TP	—	0.955	0.512	0.061	0.310	0.0189	0.059
PP		—	0.303	0.024	0.203	0.000	0.006
SP			—	0.212	0.496	0.275	0.477
PO_4				—	0.460	0.166	0.365
SRP					—	0.246	0.320
SMWP						—	0.098

TABLE 3. Correlation matrix for data from the tributaries of Lake Memphremagog showing that total phosphorus (TP) was correlated best with suspended pigment concentration (LnR). The remaining phosphorus fractions are defined in Table 2. Each correlation is based on 69 samples and, therefore, there is a significant relation only when r^2 exceeds 0.041.

	TP	PP	SP	PO_4	SRP	SMWP	LMWP
LnR	0.168	0.158	0.075	0.010	0.068	0.025	0.012
TP	—	0.911	0.497	0.411	0.404	0.419	0.010
PP		—	0.213	0.287	0.159	0.313	0.002
SP			—	0.399	0.890	0.355	0.044
PO_4				—	0.393	0.124	0.012
SRP					—	0.278	0.018
SMWP						—	0.005

concentration (LnR) yielded the highest r^2 when correlated with total P, but this correlation was not significantly better (F-test $P = 5\%$) than that between LnR and particulate P in either lake or rivers. The high correlation also reflects an inherent autocorrelation as particulate P is calculated from total P. The remaining fractions correlated less well with both total P and sestonic pigment concentration.

Multiple regression analyses did not add substantially to these results. No other P fraction had a significant effect ($P < 0.05$). Figure 1 shows the relationships between LnR and total P in Lake Memphremagog and its tributaries. The two regression lines, corrected to a geometric regression following Ricker (1973), are very similar both to each other and to that derived (Bergmann and Peters 1980) from different lakes ($R = 96 \exp(-0.018TP)$). This suggests that the relationship between total P and suspended pigments is relatively constant in freshwater.

The present regressions differ from that obtained previously in the increased residual variation indicated by the low coefficients of determination. In the lake, the low r^2 value probably reflects the less-careful method of filter preservation, the long storage time (Table 1; Bergmann and Peters 1980), and the reduced range of total P concentrations examined, which in turn reduces the proportion of the variance which can be explained by total P. In rivers, the especially low values of r^2 also indicate increased variability with respect to the lake. No one river was consistently above or below the average response, but some high values of LnR were certainly related to storms and heavy runoff which greatly increased soluble P in some rivers (Peters 1978), but did not proportionally increase the amount of colored particulates. Extremely low values of R, which reflect increases in particulate pigment without increases in P, had no obvious cause. This increased variability in river sites also appears when the

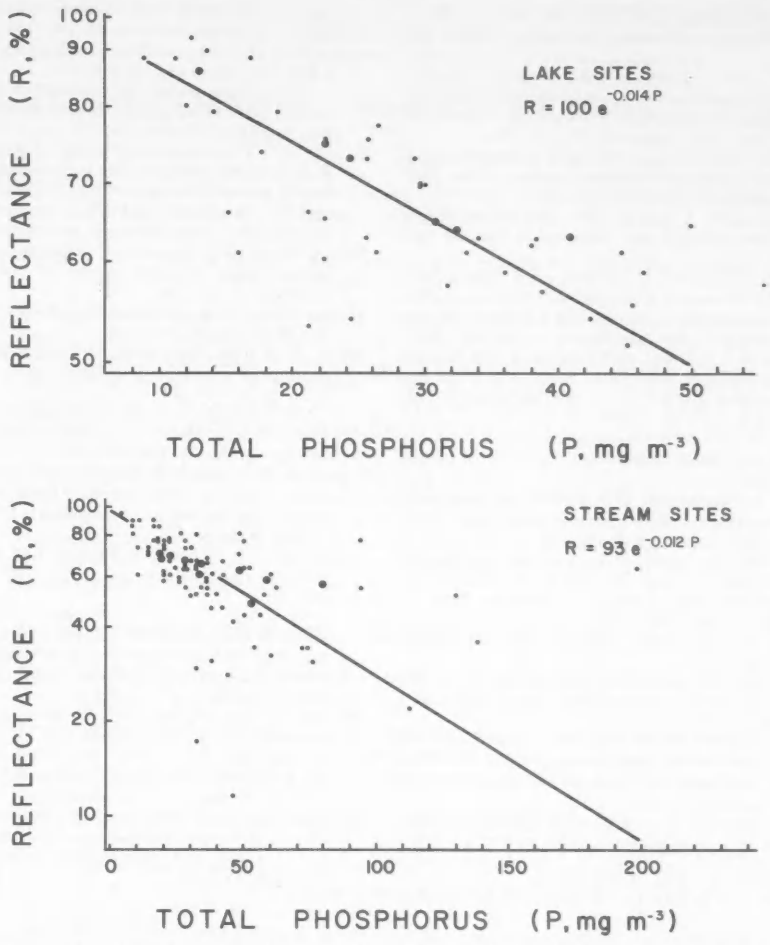

FIG. 1. The relationship between reflectance and total P concentration in Lake Memphremagog (top panel) and its tributaries (bottom panel). Oversized points indicating mean values for each site take slightly eccentric positions relative to the geometric regression lines (Ricker 1973) through the individual points. This eccentricity represents the effect of departures from normality in the regression.

correlation matrices of river and lake sites are compared: of the 28 coefficients listed in Tables 1 and 2, 19 were higher in the lake.

Within the limits of this study, total P is the most practical correlate of seston concentration. Particulate P is as adequate statistically, but the additional analytical steps required to measure particulate P make total P analysis more attractive. The remaining fractions were less effective descriptors of seston concentration. This may reflect technical difficulties in estimating the concentrations of small P fractions, but because such problems will recur in subsequent analyses these fractions must be rejected as the index of choice whatever the source of the low correlation.

Some uninvestigated fraction may well exist which correlates better with reflectance or with some other index of seston level. This study shows only that the most common fractionations do not yield better descriptions than does total P. Until this putative fraction can be found or unless reflectance can be shown to be poorly related to other parameters of lake trophic state, this analysis confirms the retention of total P as the simplest and most meaningful measure of this important nutrient in both lakes and rivers.

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The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll *a*

JOHN J. CULLEN[1]

Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791 – 803.

The relationship between chlorophyll *a* and phytoplankton biomass (organic carbon content) is highly variable as is the yield of *in vivo* fluorescence per unit chlorophyll. Thus, vertical profiles of chlorophyll or *in vivo* fluorescence must be interpreted with caution if their ecological significance is to be established. Although the variability of carbon-to-chlorophyll ratios and fluorescence yield is large, much of it can be anticipated, corrected for, and usefully interpreted. Vertical profiles from different regions of the sea are presented; each has a deep chlorophyll maximum, but the probable mechanisms of their formation and maintenance differ widely. Most vertical distributions of chlorophyll can be explained by the interaction between hydrography and growth, behavior, or physiological adaptation of phytoplankton with no special consideration of grazing by herbivores, even though vertical distributions of epizooplankton are not uniform. The interaction between vertical profiles of zooplankton and chlorophyll will be better understood when the relationships between chlorophyll and phytoplankton biomass in those profiles is determined.

Key words: chlorophyll *a*, fluorescence, phytoplankton, vertical structure

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791 – 803.

La relation entre la chlorophylle *a* et la biomasse phytoplanctonique (teneur en carbone organique), tout comme le rendement en fluorescence *in vivo* par unité de chlorophylle est fortement variable. C'est pourquoi il faut interpréter avec prudence les profils verticaux de chlorophylle ou de fluorescence *in vivo* quand il s'agit d'établir leur signification écologique. Bien que la variabilité des rapports carbone : chlorophylle et du rendement en fluorescence soit forte, on peut anticiper une bonne partie de cette variabilité, la corriger et l'interpréter d'une manière utile. Nous présentons des profils verticaux de différentes régions de la mer; chacun possède un maximum de chlorophylle en profondeur, mais il y a de grandes différences dans les mécanismes probables de leur formation et de leur maintien. On peut expliquer la plupart des distributions verticales de la chlorophylle par l'interaction entre les caractéristiques hydrographique croissance, le comportement ou l'adaptation physiologique du phytoplancton, sans accorder d'importance spéciale au broutage par les herbivores, même si la distribution verticale des épizooplanctontes n'est pas uniforme. On comprendra mieux l'interaction entre les profils verticaux du zooplancton et de la chlorophylle quand on aura trouvé les relations entre la chlorophylle et la biomasse phytoplanctonique dans ces profils.

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A convenient, accurate and precise measure of phytoplankton biomass is essential to most studies of biological processes in epipelagic communities. The index of choice in recent decades, the concentration of chlorophyll *a*, was supplemented by *in vivo* chlorophyll fluorescence (Lorenzen 1966). Continuous measurements of *in vivo* fluorescence at sea produced much information about the horizontal patterns of phytoplankton upon which theoretical work advanced rapidly (Herman and Platt 1980). Concurrently, more and better observations of the vertical distributions of chlorophyll *a* and *in vivo* fluorescence were collected. A feature of many profiles collected from diverse regions is a subsurface chlorophyll maximum (Anderson 1972; Venrick et al. 1973; Cullen and Eppley 1981; Ortner et al. 1980). In this commentary, it

[1]Address after June 1, 1982: University of Texas, Port Aransas Marine Laboratory, Port Aransas, TX 78373, USA.

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is shown that although deep chlorophyll maxima are common to profiles from many regions, they probably arise from several different causes. It is further shown that vertical profiles of chlorophyll or fluorescence must be interpreted with great care if their significance for the economy of the pelagic food web is to be established.

Measuring the Biomass of Phytoplankton

What is Biomass?

Biomass is defined as the amount of living material, but for practical and theoretical reasons, units have not been rigidly prescribed. Instead, "biomass' has become a catch-all term with the operational definition, "the amount of biological material that is of interest to the researcher." The word is convenient and unlikely to be abandoned, but its meaning, at least within the field of planktonic ecology, is nebulous almost to the point of uselessness. Thus, any discussion of biomass should include a specific definition and should have a justification of the choice.

The concentration of organic carbon associated with phytoplankton (usually expressed as $mg \cdot m^{-3}$) is commonly used to express the amount of phytoplankton, but phytoplankton have also been considered in terms of nitrogen (Pavoni 1969; Wroblewski 1977) or phosphorus (Perry and Eppley 1981) content. The cell volumes of phytoplankton have been calculated by different methods, and biomass has been obtained by applying conversion factors (cf. Smayda 1978). The concentration of chlorophyll *a* is often determined to estimate phytoplankton abundance, and many researchers refer to chlorophyll as an index or indicator of phytoplankton biomass. For some studies concerned primarily with photosynthesis, chlorophyll concentration *per se* is the relevant quantity upon which theoretical generalizations can be constructed (cf. Bannister and Laws 1980). For the purposes of this discussion, however, biomass will be defined as the amount of organic carbon (cf. Strickland 1965). Organic carbon concentration is a good index of the caloric content of phytoplankton and is thus an appropriate unit of biomass for studying fluxes of energy, an important step in the analysis of the dynamics of ecosystems (Platt and Irwin 1973). Also, the concentration of organic carbon associated with phytoplankton must be known to calculate growth rates from measurements of primary production.

Unfortunately, it is impossible to measure directly the organic carbon content of natural phytoplankton free of contamination from detritus and heterotrophic microplankton (Banse 1977). Indirect methods using biomass indicators or experimental manipulations must be used to estimate phytoplankton carbon in natural samples (Eppley 1968; Eppley et al. 1977; Redalje and Laws 1981).

Estimating the Biomass of Phytoplankton: Chlorophyll *a*

The concentration of chlorophyll *a* is still the best chemical indicator of phytoplankton biomass in natural samples. Quite simply, photosynthetic organisms have it, others don't. However, the interpretation of chlorophyll measurements has important limitations. Chlorophyll represents only about 1% of the dry weight of a phytoplankton cell, and the proportion can be quite variable (Strickland 1965; Shuter 1979). To those interested in chlorophyll concentration as a measure of food for herbivores, it should be clear that chlorophyll is present only in trace quantities. Zooplankters do not subsist on chlorophyll. Therefore, by themselves, distributions of chlorophyll cannot necessarily be considered as good indices of the distribution of food available to secondary producers.

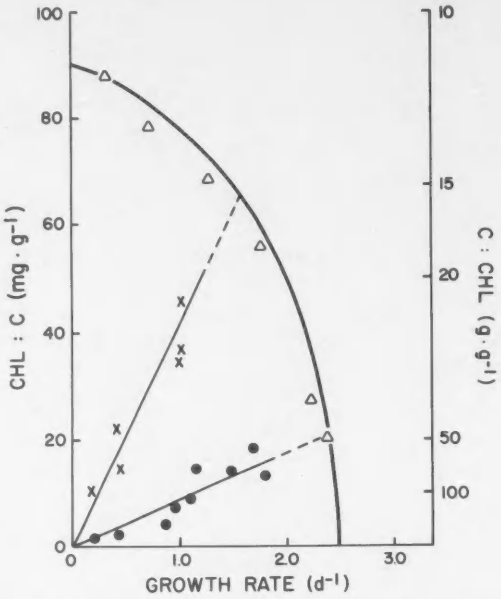

FIG. 1. The relationship between chlorophyll-to-carbon ratio (not C:Chl) and growth rate. Triangles, nutrient-saturated (light-limited) growth of *Chlorella pyrenoidosa* (Myers and Graham 1971); ×, nutrient-limited growth of *Thalassiosira pseudonana* at 0.07 $cal \cdot cm^{-2} \cdot min^{-1}$ and 12-h photoperiod (Eppley and Renger 1972; Perry 1976); circles, nitrate-limited growth of *T. pseudonana* at 0.1 $cal \cdot cm^{-2} \cdot min^{-1}$ continuous light (Caperon and Meyer 1972). In both light regimes, Chl:C is a linear function of nutrient-limited growth rate within the limits of precision, but at the lower irradiance the slope is steeper. The curve was calculated from a model presented by Bannister and Laws (1980), the source of this figure. C:Chl conversions are added for convenience.

Often, chlorophyll concentration is measured, but the desired datum is the organic carbon content of the phytoplankton. The necessary conversion is made by multiplying chlorophyll concentration by the carbon-to-chlorophyll ratio (C:Chl, $g \cdot g^{-1}$; cf. Eppley 1972; Banse 1977). Unfortunately, the ratio is by no means constant.

In laboratory experiments a wide variation of C:Chl has been demonstrated, and Shuter (1979) has modeled such changes in cellular composition. Within one strain of phytoplankton, C:Chl can vary more than fourfold as a function of nitrogen limitation (Bannister and Laws 1980; Goldman 1980). With adequate nutrients, the ratio is strongly correlated with growth irradiance (Bannister and Laws 1980) and also shows a temperature effect (Eppley 1972; Yoder 1979).

Under similar culture conditions, C:Chl for dinoflagellates is much higher than for diatoms (Chan 1980). The chlorophyll content of phytoplankton, usually measured as chlorophyll per cell, varies by about a factor of 2 with time of day (reviewed by Sournia 1974). Because carbon uptake is confined to the light period and chlorophyll synthesis may proceed in the dark, diel variation of C:Chl may be moderate to significant (Sournia 1974). Eppley et al. (1971) presented data which showed a diel variation of C:Chl of about ±25%.

The many sources of variation in C:Chl can combine to produce carbon-to-chlorophyll ratios as low as about 10 (Laws and Bannister 1980) or as high as 250 or more (Holmes et al. 1967; Sakshaug and Holm-Hansen 1977; Malone and Chervin 1979; Laws and Bannister 1980; Redalje and Laws 1981). Enough information on this variation exists to allow a mathematical description of the relationship between C:Chl and nutrient- or light-limited growth of phytoplankton (Bannister and Laws 1980; Fig. 1). There is a strong correlation between C:Chl and the relative growth rates of the algae that have been studied (Bannister and Laws 1980; Goldman 1980), and as Goldman has pointed out, the carbon-to-chlorophyll ratio is an informative index of the nutritional state of natural populations.

Because the range of possible C:Chl ratios is so large, it is not surprising that chlorophyll distributions may have patterns that are independent of the distributions of phytoplankton biomass. For instance, features of the euphotic zone in stratified water columns can influence C:Chl in such a way as to create a deep chlorophyll maximum (Steele 1964). Phytoplankton near the surface, where irradiance is high and nutrient concentrations are low, have minimal chlorophyll content. At depth (near the nitracline), decreasing irradiance and an increasing nitrate supply stimulate increases in chlorophyll relative to phytoplankton carbon, potentially by a factor of 10 or more. Temperature acts in the opposite direction, but presumably the effect is not as strong. An example will be presented in a following section.

Fluorescence *in vivo* as a Measure of Chlorophyll

Having recognized the uncertainty of the chlorophyll:phytoplankton biomass relationship, we can examine the next level of variability, fluorescence yield per chlorophyll molecule *in vivo*.

The fluorescence of chlorophyll *a in vivo* is measured by irradiating with blue light a sample of water containing phytoplankton and measuring the red light fluoresced by chlorophyll molecules. Ideally, the amount of fluorescence would be linearly related to the concentration of chlorophyll in any sample. In fact, this is not the case: fluorescence is a small and variable percentage of the light absorbed by the photosynthetic apparatus, and the capacity of the chlorophyll to absorb light is also variable (Harris 1978; Kiefer 1973b).

The variability of fluorescence yield in phytoplankton reflects the complex control of both the light absorption and of the disposition of energy in the photosynthetic apparatus (reviewed by Harris 1978; Prézelin 1982). Early studies of *in vivo* fluorescence in oceanographic contexts showed that characterization of this variability as a function of species composition, nutrition, and preconditioning could have value well beyond that of merely increasing the precision of the method (Strickland 1968; Blasco 1973; Kiefer 1973a, b; Yentsch 1974a). True to these expectations, results of recent studies of *in vivo* fluorescence have been quite provocative (cf. Harris 1978; Vincent 1980; Prézelin 1982).

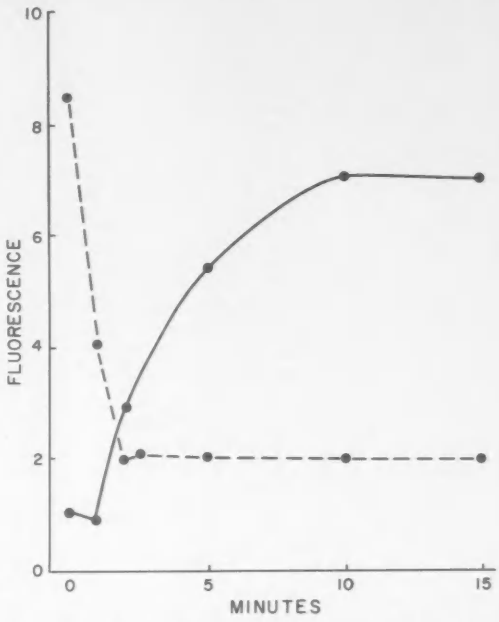

FIG. 2. Time course of fluorescence inhibition and recovery (Lake Windemere, U.K.). Fluorescence is the peak measurement from the first 5 s in the fluorometer. The solid line represents surface water exposed to dim light over 15 min. The broken line represents 5 m water exposed to bright light (1500 $\mu E \cdot m^{-2} \cdot s^{-1}$) over 15 min. From Vincent (1979).

The ratio of fluorescence to chlorophyll *a* (*R*) increases with nutrient starvation of phytoplankton (Blasco 1973; Kiefer 1973b; Sakshaug and Holm-Hansen 1977) and can also show considerable variability among taxa: at least fivefold among eukaryotic microalgae grown under identical conditions (Strickland 1968). The cyanobacteria have lower fluorescence yields (Heaney 1978). Changes of *R* can produce easily measured, coherent patterns which can lead to inferences about processes important to primary production (Herbland and Voituriez 1977a). For instance, a transect of fluorescence and chlorophyll taken perpendicular to the Southern California coast (Kiefer 1973a) showed large differences in *R* between inshore and offshore water. In the latter, chlorophyll concentration is lower than, species composition is different from (Reid et al. 1978; Cullen 1980), and nutrient limitation is presumably more severe than in nearshore waters (Eppley 1968; Kiefer 1973a).

Fluorescence yield is very responsive to ambient light and can change rapidly when shifts in irradiance are experienced by phytoplankton (Heaney 1978; Harris 1978; Vincent 1979). Fluroescence can undergo changes on different time scales during measurement with a fluorometer (Kiefer

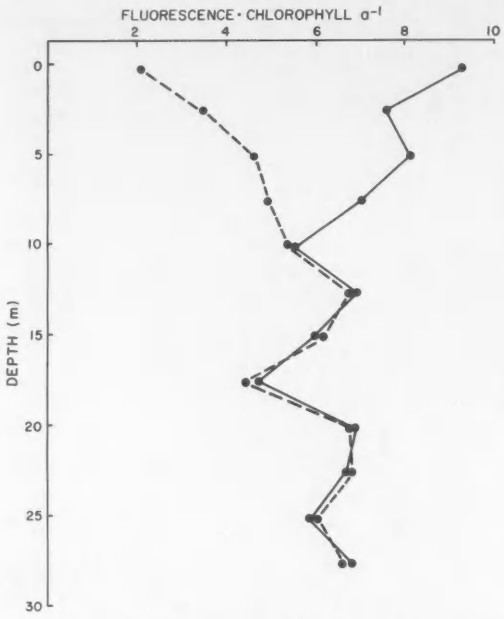

FIG. 3. Photoinhibition of fluorescence in a vertical profile (Lake Okareka, New Zealand). The broken line indicates fluorescence yield measured immediately upon collection. The solid line connects measurements made on the same samples after 2 h in complete darkness. From Vincent (1979).

1973b; Vincent 1979) and can show strong, reversible photoinhibition which is expressed on time scales of seconds to minutes (Heaney 1978, Vincent 1979; Fig. 2). Inhibition of fluorescence near the surface could possibly produce subsurface fluorescence maxima that do not represent chlorophyll maxima (Fig. 3). There are some indications that photoinhibition of fluorescence, which can decrease R by a factor of 8, is more strongly expressed among the diatoms as compared to other phytoplankton (Loftus and Seliger 1975; Harris 1978; Heaney 1978).

Diel changes in fluorescence yield have been observed in the laboratory and in the field. The dinoflagellate *Gonyaulax polyedra* grown under the relatively low-irradiance conditions of laboratory incubators has a circadian rhythm of fluorescence yield that is in phase with a rhythm of photosynthetic capacity, which is highest during the light period (Sweeney et al. 1979, see also Prézelin and Ley 1980). However, natural samples from near the sea surface may show an inverse pattern of fluorescence yield, forced by the photoinhibitory effects of bright sunlight (Kiefer 1973a; Yentsch 1974a; Loftus and Seliger 1975).

These observations make it clear that patterns of fluorescence, independent of variations in chlorophyll concentration (much less phytoplankton biomass) may be found wherever the sampling program encounters changes in light, nutrients, species composition, or time of day. Also, the type of fluorometer can determine in part the pattern observed (Vincent 1979, 1981; Harris 1980; Prézelin and Ley 1980): light histories of the phytoplankton and methods of measurement interact to produce different information from *in situ* fluorometry, continuous flow fluorometry, and dark-adapted discrete determinations of *in vivo* fluorescence.

Slovacek and Hannan (1977) suggested that addition of the photosynthetic inhibitor [3-(3,4-dichlorophenyl)-1,1-dimethylurea] (DCMU) to a sample would elevate fluorescence yield to a constant, maximal level, but subsequent studies have shown DCMU-treated fluorescence is strongly affected by light history (Harris 1980; Vincent 1980) and has a diel periodicity of greater magnitude than that of untreated *in vivo* fluorescence (Prézelin and Ley 1980).

One other aspect of uncertainty in fluorescence and chlorophyll measurements concerns the presence of chlorophyll degradation products in natural samples: these pigments may appear to be chlorophyll *in vivo* and in analysis of extracted samples. The relative contribution of these products is greater at depth, and the analysis of the full pigment fraction allows useful ecological interpretation (Gieskes et al. 1978; Jeffrey and Hallegraeff 1980).

Implications of Variability in Chlorophyll Content and Fluorescence Yield of Phytoplankton

The potential for variability of fluorescence and chlorophyll as measures of phytoplankton biomass is staggering, but the imprecision has been tolerated because the information content of fluorescence profiles is so great. I suggest that the imprecision should not be merely tolerated: it should be anticipated, recognized, corrected for, and most importantly, interpreted. Pooling data from many vertical profiles for regression analysis may be valid for some applications, but it ignores systematic variation within profiles that may have significant information content (cf. Yentsch 1974a; Eppley et al. 1977; Herbland and Voituriez 1977a; Harris 1980; Cullen and Eppley 1981).

The parameters I have been discussing are functions of light, nutrients, and species composition; frequently, all of them change sharply near the deep chlorophyll maximum. Vertical profiles should sample these variations efficaciously; therefore, to get a good picture of the important features in a vertical profile, precise measurements with high spatial resolution should be obtained, especially near the nutricline and deep chlorophyll maximum.

The Vertical Structure of Phytoplankton in Divers Environments

Just as it is misleading and unjustified to assume that fluorescence yield or C:Chl is uniform in space or time, it is also incorrect to assume that the vertical structure of marine phytoplankton is determined by the same processes in different environments. In this section I present a number of vertical profiles and will speculate on the mechanisms of their formation and maintenance.

Vertical Profiles from Relatively Stable Systems: Typical Tropical Structure

Low seasonal variation allows more temporal constancy of planktonic processes in the tropics as compared to higher latitudes (Cushing 1981) even though the effects of hydrogra-

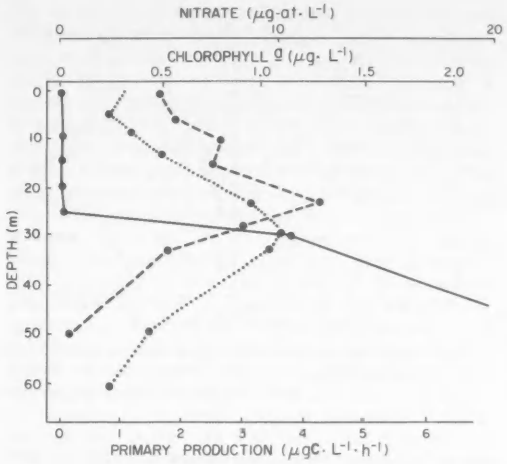

FIG. 4. Vertical profiles from the Guinea Dome, 20°50′W, 11°30′N, August 1973. Broken line, primary production; dotted line, chlorophyll *a*; solid line, nitrate. From Voituriez and Dandonneau (1974).

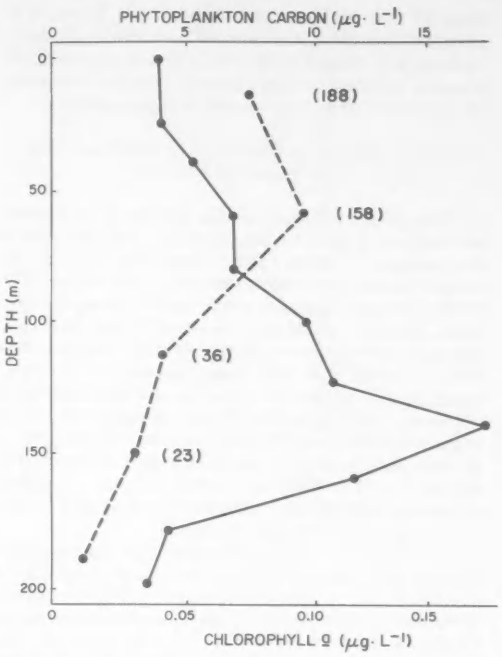

FIG. 5. Vertical profiles from the North Pacific Central Gyre, June 22, 1973. Broken line, phytoplankton carbon concentration estimated from microscopic examination of preserved samples; solid line, chlorophyll *a*. Carbon-to-chlorophyll ratios are enclosed in parentheses. From Beers et al. (1975).

phy (currents, upwelling) and climate (monsoons, winds) are appreciable and seasonal (Sournia 1969; Vinogradov 1981). Because of the relatively small magnitude of fluctuations of standing stocks and the balance (*sensu* Heinrich 1962) between phytoplankton and zooplankton characteristic of unperturbed tropical regions, vertical profiles from low-latitude environments are more likely to reflect steady-state balances of fluxes which can be estimated from measurements *in situ*, rather than relicts of earlier, transient events.

The close and relatively stable coupling between physical and biological processes in the eastern tropical Atlantic Ocean has permitted the characterization of hydrographic and biological features into "typical tropical structure" (TTS; Herbland and Voituriez 1979). In a number of papers, it has been shown that TTS is a continuum of pattern, ultimately controlled by the input of nutrients from below, nutrients supplied by upwelling (Vinogradov 1981) or turbulent mixing (Kaiser and Postel 1979; Voituriez and Herbland 1979; Herbland and le Bouteiller 1982).

With the exception of "atypical" (Herbland and Voituriez 1977a) regions affected by lateral input of nutrients from nearby equatorial upwelling, most vertical profiles from the eastern tropical Atlantic Ocean have the general shape depicted in Fig. 4. The features of vertical profiles have definable relationships with the thermal structure of the water column, but from an ecological perspective, nutrient distributions are more important: the chlorophyll maximum is found near the nitracline and the peak in primary production is coincident with (according to Herbland and Voituriez 1979) or just above (Guinea Dome measurements by Voituriez and Dandonneau 1974) the chlorophyll maximum. Primary production and chlorophyll concentration in the water column are inversely related to depth of the nitracline (Herbland and Voituriez 1979); the oligotrophic extreme of TTS is characterized by a deep thermocline and nitracline, low chlorophyll concentrations, and minimal primary production; and hydrographic and biological features change together along the continuum, culminating in the productive extreme of TTS : shallow thermocline and nitracline, high chlorophyll and production (Herbland and Voituriez 1979). If the nutrient flux is sufficient to elevate nitrate concentrations in the surface-mixed layers, TTS breaks down.

Even if hydrographic structure changes rather abruptly (temporally or spatially) due to variations of mixing from below, TTS can be maintained, as measurements at stations affected by the meandering Lomonosov current have shown (Herbland and le Bouteiller 1982).

It appears that only one dimension (the vertical) need be considered to explain much of the variability in typical tropical structure, and indeed, profiles like Fig. 4 are similar to the later stages of time-dependent simulation models which consider only the vertical dimension (Jamart et al. 1977; Menshutkin and Finenko 1977): the subsurface chlorophyll maximum is maintained primarily as a result of enhanced primary production in a stratum.

Shoal thermoclines in the tropics are indicative of upwelling or high turbulence from below, and the negative correlation between integrated primary production and depth of the thermocline in TTS (Herbland and Voituriez 1979) is consistent with the hypothesis that vertical inputs of nutrients or energy have a dominant effect on primary production (cf.

Margalef 1978; McGowan and Hayward 1978; Eppley et al. 1979; Herbland and le Bouteiller 1982; see also an alternative explanation by Yentsch 1974b, 1981). Thus discussions of the processes important to "typical tropical structure" are probably relevant to other stable systems in higher latitudes.

A Vertical Profile of Chlorophyll that Does Not Represent Phytoplankton Biomass

Although subject to more seasonal variation of wind mixing and irradiance than the tropics, the great central gyres, and in this example, the North Pacific Central Gyre (Fig. 5), are certainly stable environments (McGowan and Walker 1979; Weiler 1980 and references within each). Chlorophyll concentrations and conventionally measured primary production rates are relatively low, and the nitracline is deeper than 100 m (Venrick 1979, and references therein). Mixing processes in this oligotropic region are not well understood (McGowan and Hayward 1978), but experimental evidence suggests that the fluxes of nutrients into the euphotic zone are probably about as low as in any oceanic environment (Eppley and Peterson 1979), and it may be proposed that a profile from a central gyre represents a situation beyond the oligotrophic extreme of "typical tropical structure."

The problem of variable chlorophyll content of phytoplankton becomes acute when profiles from the North Pacific Central Gyre are studied. If a chlorophyll profile is compared to the depth distribution of phytoplankton carbon determined by microscopic examination (Fig. 5), it becomes clear that concentration of chlorophyll is a poor indicator of phytoplankton biomass indeed (cf. Kiefer et al. 1976). The chlorophyll maximum represents a physiological adaptation to the lower irradiance and to the greater availability of nutrients in that stratum, and changes in C:Chl (Fig. 5) are entirely consistent with those measured in controlled experiments (Fig. 1). Interestingly, the ratios suggest nutrient limitation of algal growth near the surface (see McCarthy and Goldman 1979; Goldman et al. 1979; Jackson 1980; Sharp et al. 1980 for discussion of this contentious subject). As postulated by Steele (1964), this chlorophyll profile from a stable environment changes independently from phytoplankton biomass.

If the profile from the North Pacific Central Gyre (Fig. 5) represents the oligotrophic extreme of a spectrum of vertical structure, and at that end of the spectrum chlorophyll is not indicative of phytoplankton, one must address the question, at what point in the change toward eutrophy does a chlorophyll profile correspond to phytoplankton biomass? Steele's (1964) model could predict most distributions of chlorophyll in the tropics with the assumption of vertically uniform distributions of phytoplankton. However, Herbland and le Bouteiller (1982) have measured particulate phosphorus along with chlorophyll for their profiles and found similar vertical structures for each. An intermediate situation is presented by Herbland and Voituriez (1977b). (See Perry and Eppley (1981) for a discussion of particulate phosphorus as an indicator of biomass, but also Strickland (1965), Sakshaug and Holm-Hansen (1977), and Maestrini and Kossut (1981) for examples of variation of C:P in phytoplankton.) More profiles of chemical constituents and phytoplankton enumerations must be compared with chlorophyll measurements before safe generalizations can be made about the vertical distributions of phytoplankton in diverse stable environments.

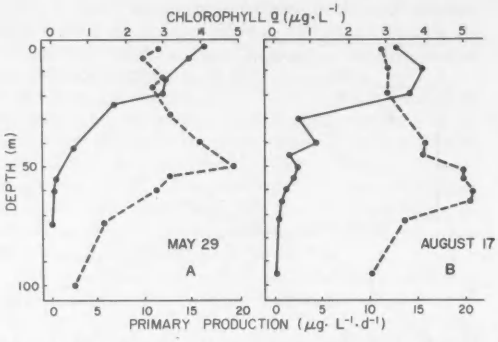

FIG. 6. Vertical profiles of *in situ* primary production (solid line) and chlorophyll *a* (broken line) at a station off the Oregon coast, 44°40′N, 127°00′W. A. May 29, 1969. B. August 17, 1969. From Anderson (1972).

Vertical Structure of Variable Environments: Transients and Relicts

In temperate latitudes, seasonal variation is expressed in irradiance, wind-induced mixing, and in some regions, upwelling. Through the seasons, then, the biomass, vertical distributions, and species composition of phytoplankton can be quite variable. Vertical profiles measured in such environments may reflect transient conditions or relict properties from prior, unobserved events.

In contrast to "typical" examples from the tropics, vertical profiles from temperate latitudes often show a near-surface peak in primary production which is to be expected during the spring bloom, but which persists through the summer, well removed from the subsurface nitracline and the chlorophyll maximum (cf. Anderson 1969; Cullen and Eppley 1981; Ortner et al. 1980; Fig. 6). Measurements have been made which confirm the inference that regeneration of nitrogenous nutrients must be higher near the surface in these environments (Harrison 1978). What process is responsible for concentrating regenerative activity near the surface, and why doesn't it act in the tropics? Perhaps the annual input of nutrients to the mixed layer each winter in temperate latitudes is retained near the surface by regenerative processes whereas deep mixing generated from above does not occur in the "typical tropical" environment, thus confining the primary production maximum to the vicinity of the nitracline. The example of the North Pacific Central Gyre (Fig. 5) is problematic, because there is little evidence that wind mixing ever reaches the nutricline (McGowan and Hayward 1978).

Significant primary production above the nitracline, which I have suggested is due to temporally distant events in temperate waters, is observed in "atypical" tropical regions and is attributed to spatially remote equatorial upwelling, which enhances production in the mixed layer by lateral transport (Herbland and Vroituriez 1977a; see also Vinogradov et al. 1971).

Just as the near-surface primary production maximum

(Fig. 6) may be a relict of nutrient input to the mixed layer months before, the chlorophyll maximum may be an accumulation of phytoplankton which was produced in overlying waters. This concept has received theoretical treatment. A term for sinking of phytoplankton was included in the mathematical model of Riley et al. (1949), and subsurface chlorophyll maxima were simulated. Jerlov (1959) suggested that physical features could dominate over biological processes in determining the vertical distributions of particles (phytoplankton): sinking particles would concentrate on density gradients. However, Steele and Yentsch (1960) presented calculations which showed that density changes in the water alone could not explain chlorophyll maxima at the foot of the euphotic zone. Steele and Yentsch suggested that physiologically induced changes in the buoyancy of phytoplankton, a response to increased nutrient supply and decreased irradiance near the bottom of the euphotic zone, could produce the observed distributions of chlorophyll.

The profiles in Fig. 6 may reflect the importance of sinking to chlorophyll profiles. The chlorophyll maximum coincides with the nitracline, exactly where one would expect to find a local maximum in primary production (Menshutkin and Finenko 1977), a decrease in C:Chl (Steele 1964), and an accumulation of sinking phytoplankton (Steele and Yentsch 1960). Anderson's (1969, 1972) papers satisfied the first two expectations, but the degree to which the chlorophyll maximum represents a decrease in the sinking rate of phytoplankton is unknown. If not supplied from above, could the chlorophyll maximum be maintained?

Vertical profiles from the Atlantic have been interpreted to suggest that chlorophyll maxima are found at depths where sinking particulate matter accumulates (Ortner et al. 1980), but falsifiable hypotheses concerning the sinking of phytoplankton and deep chlorophyll maxima have not been tested thoroughly with data from the field. Quantification of vertical fluxes is necessary (cf. Bienfang 1980).

Probably the most likely situation for chlorophyll profiles to be dominated by the effects of depth-differential sinking of phytoplankton would be after the spring bloom in temperate latitudes when sedimentation rates of phytoplankton should exceed growth rates (cf. Smetacek et al. 1978); thus subsurface chlorophyll maxima composed of diatoms could appear as transient features. An example from the western edge of the California Current (30°N, 120°W; Venrick et al. 1973), where chlorophyll profiles were collected throughout the year, is consistent with explanations invoking the sinking of phytoplankton, but species composition was not reported and definite conclusions cannot be drawn.

The Direct Influence of Density Gradients on the Vertical Distributions of Phytoplankton

On a finer vertical scale, Derenbach et al. (1979) have described chlorophyll maxima which seem to reflect an interaction between the microscale physical structure of the thermocline (cf. Woods and Wiley 1972) and the sinking of diatoms (*Skeletonema costatum*) apparently independent of physiological changes in buoyancy (Fig. 7). The interaction of horizontal shear and horizontal patchiness could also contribute to the observed pattern (G. A. Riley, Dalhousie

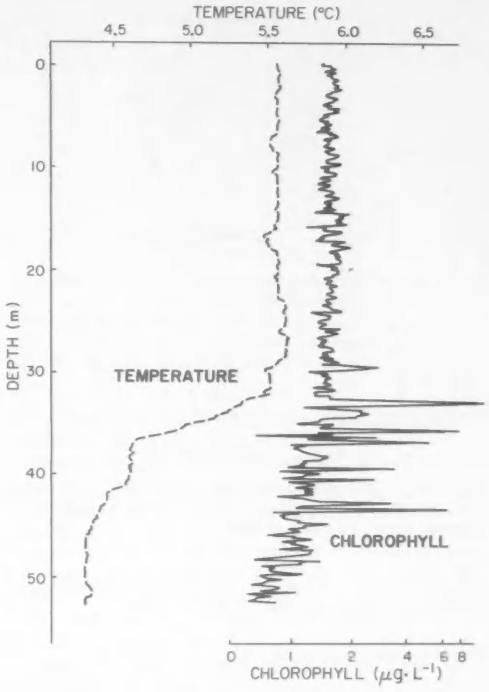

FIG. 7. Vertical profile of temperature and chlorophyll *a* (from an *in situ* fluorometer), Baltic Sea. Intense peaks of chlorophyll correspond with microscale density structure (from Derenbach et al. 1979).

University, Halifax, N.S., personal communication). The example in Fig. 7 emphasizes the utility of making high-resolution fluorescence measurements with equally good determination of physical structure. Until this is done more frequently, it will be difficult to know how commonly physical factors have overriding influence on the vertical distributions of phytoplankton. Microscale chlorophyll maxima were not found in another region of the Baltic where the thermocline was less well developed (Derenbach et al. 1979), nor have they been observed during recent cruises in the Southern California Bight (R. W. Eppley, Scripps Institution of Oceanography, La Jolla, CA 92093, USA, personal communication).

To the best of my knowledge, the exact coincidence of chlorophyll maxima and maximum density or temperature gradients in oceanic water columns has been examined explicitly with statistical methods only twice, with negative results for both the western Indian Ocean (Karabashev and Solov'yev 1978) and the Southern California Bight (Cullen and Eppley 1981). The negative results based on data with a resolution of meters do not imply that physical processes have little control over the vertical distribution of chlorophyll, nor do they say that chlorophyll maxima are not in the pycnocline, only that factors other than density structure are of greater proximate

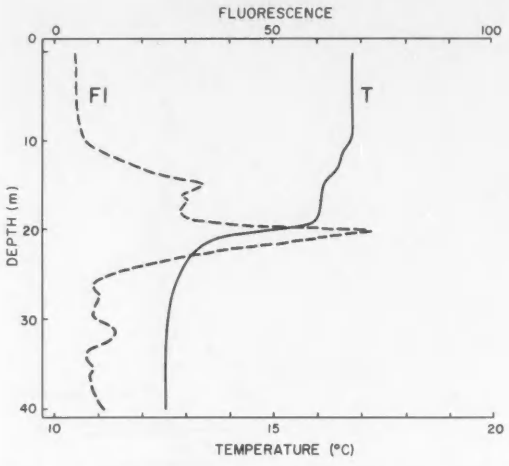

FIG. 8. Vertical profile of fluorescence (arbitrary units) and temperature from the western English Channel, 5°23′W, 49°25′N, July 1975. From Pingree et al. (1975).

importance (see a discussion on the thermocline/nitracline relationship in Herbland and Voituriez 1979).

ENVIRONMENTS WHERE DENSITY GRADIENTS AND BIOLOGICAL PROCESSES CONTRIBUTE TO VERTICAL STRUCTURE

Excellent examples of the interaction between density structure and biological processes can be found near tidally influenced frontal systems. Pingree et al. (1975) have discussed the development of high concentrations of dinoflagellates within sharp density gradients near frontal boundaries and have explained the increase of phytoplankton abundance in the thermocline in terms of stability: phytoplankters above the thermocline are well mixed in a nutrient-depleted surface layer where conditions for growth are unfavorable, and those organisms below the thermocline are in a turbulent regime in which mean irradiance is too low for growth. Phytoplankton in the thermocline attain high concentrations because the characteristic mixing time of the water is considerably longer than the algal generation time, allowing growth and accumulation. Vertical profiles of fluorescence and temperature from the English Channel offer strong support for the stability–growth hypothesis (Pingree et al. 1975; Fig. 8). The extent to which the aggregation of phytoplankton in the thermocline is behaviorally determined (cf. Falkowski et al. 1980; Cullen and Horrigan 1981; Heaney and Eppley 1981) has not been assessed, although Holligan (1978) has looked for, but not found, evidence for diurnal vertical migration.

CHLOROPHYLL MAXIMA AND PHYTOPLANKTON BEHAVIOR

Phytoplankton can do more than grow, sink, or be consumed. Behavioral mechanisms which determine vertical position in the water column are common among unicellular

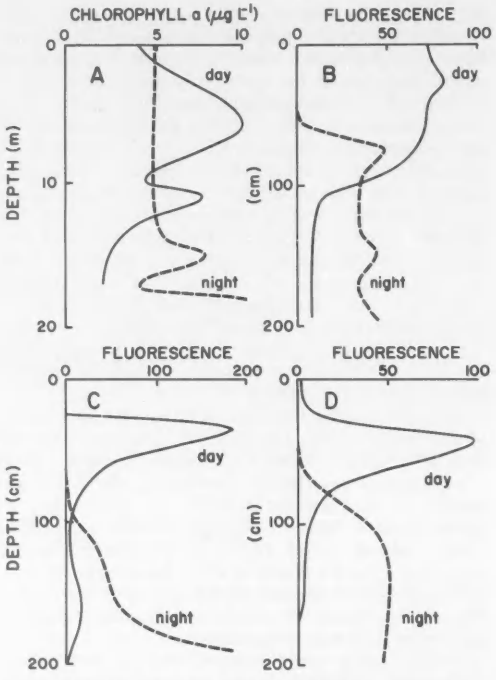

FIG. 9. Behavior of the naked dinoflagellate, *Gymnodinium sanguineum* (= *splendens*) A. Vertical profiles from "isothermal" Coyote Bay, Gulf of California (Kiefer and Lasker 1975). B–D, Vertical profiles from a 2.0-m enclosed water column in the laboratory, surface irradiance, 900 $\mu E \cdot m^{-2} \cdot s^{-1}$ on a 12-h light:12-h dark cycle: B, nitrate greater than 1 μM throughout; C, nitrate depleted throughout; D, nitrate greater than 1 μM only near the bottom of the tank. From Cullen and Horrigan (1981).

algae: motile phytoplankton can migrate vertically (Forward 1976) or aggregate in thin layers (Falkowski et al. 1980; Harris et al. 1979), blue-green algae (cyanobacteria) can move vertically by physiologically altering buoyance (Walsby and Klemer 1974), and diatoms can aggregate near a nutrient gradient by modifying their sinking rate (Steele and Yentsch 1960).

The diurnal vertical migration of dinoflagellates, classically characterized as phototactic (Hasle 1950; Forward 1976), also involves geotaxis and a diel rhythm (cf. Eppley et al. 1968; Weiler and Karl 1979; Cullen and Horrigan 1981; Kamykowski 1981). Kiefer and Lasker's (1975) measurements on a phytoplankton assemblage dominated by the dinoflagellate, *Gymnodinium sanguineum* (= *splendens*) provide an example (Fig. 9a). However, dinoflagellates are not constrained to one behavioral response: different species may have their own preferred depths during the day (Hasle 1950; Blasco 1978), and the behavioral patterns of organisms of the same species may change with nutrient availability (Eppley et al. 1968; Heaney and Eppley 1981; Cullen and Horrigan 1981; Fig. 9, B–D). Thus, behavior of phytoplankton may

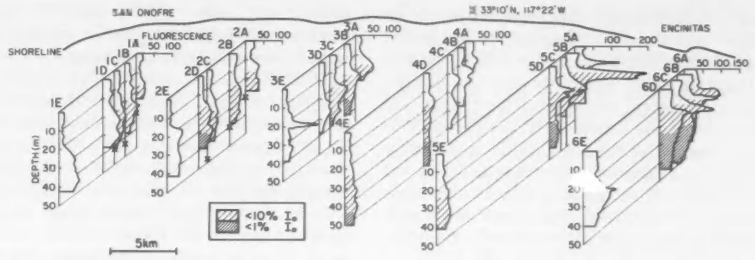

FIG. 10. Vertical profiles of fluorescence and light penetration (where measured) Southern California Bight, August 1978. Hatch marks represent percentage of surface irradiance, I_o. The 1% light level is designated by an × at those stations where it was reached. Stations are labeled 1A–E, 2A–E, etc. The letters A, B, C, D, E correspond to water depths of 30, 50, 100, 300, and 750 m, respectively. This figure shows that most of the subsurface maxima were near the 10% light level. In addition, most were near the nitracline. From Cullen (1980).

contribute significantly to a variety of vertical profiles of chlorophyll (cf. Kamykowski 1980).

CHLOROPHYLL PROFILES FROM A HORIZONTALLY HETEROGENEOUS REGION

The examples of vertical profiles given so far represent a spectrum of factors that promote formation or maintenance of deep chlorophyll maxima. In most examples, some factors are clearly more important than others. In environments with considerable horizontal heterogeneity, the situation can be much more complicated.

A 25 km × 40 km grid near the southern California Coast was sampled in 2 d for fluorescence, chlorophyll, nutrients, and phytoplankton enumeration (Cullen 1980). Inspection of the fluorescence and chlorophyll data revealed that a subsurface chlorophyll maximum was present at each station, near the nitracline and 10% light level (Fig. 10). Chlorophyll concentrations were higher and subsurface peaks more pronounced nearshore and to the south. Still, little could be inferred from the distributions of chlorophyll and fluorescence alone: the shapes of the profiles, magnitudes of the chlorophyll peaks, and relationships between chlorophyll and nutrients or light varied over a range that was similar to that encountered in the Southern California Bight over 4 yr (cf. Cullen and Eppley 1981).

Microscopic examination of preserved samples from the grid provided the information necessary to interpret the patterns observed. Phytoplankton carbon estimates from microscopic examination (Eppley et al. 1977) revealed that at 16 of the 30 stations, concentrations of phytoplankton at the surface were greater than in the chlorophyll maximum. At the 14 stations nearshore and to the south, the chlorophyll maxima were dominated by relatively large motile dinoflagellates, especially *Ceratium tripos* (cf. Falkowski et al. 1980), and had higher concentrations of phytoplankton carbon than at the surface. Even though calculating concentrations of phytoplankton carbon from examination of preserved samples has its uncertainties, the carbon-to-chlorophyll ratios from this data set were, like those from the North Pacific Central Gyre (Fig. 5), quite consistent with experimental observations: in nitrate-depleted surface waters, the ratio was 92. Where the chlorophyll maximum represented a physiological change in C:Chl, it was 25. The chlorophyll maximum layer dominated by dinoflagellates had a characteristic C:Chl of 70.

Although diatoms were not numerically important in this study, they showed a significant pattern: they were more concentrated in the chlorophyll maxima throughout the grid, consistent with other observations from temperate latitudes (Venrick et al. 1973), and this probably involved changes in sinking rate near the nitracline (cf. Steele and Yentsch 1960).

Thus, in one small sampling region, a variety of chlorophyll maximum "types" were found, each with its own ecological interpretation. Unfortunately, labor-intensive measurements were required to reveal the nature of the chlorophyll maxima. In similar studies concerned with more general questions, a few samples for phytoplankton enumeration and particle counts or analysis of particulate matter could have provided much useful information with considerably less work.

Classification of Deep Chlorophyll Maxima

The foregoing presentation has demonstrated that all subsurface chlorophyll maxima are not the same, and many can be categorized by the mechanisms of their formation and maintenance. To conclude, I will list some "types" of deep chlorophyll maxima and speculate on the implications for sampling and interpretation.

Primary production maximum and chlorophyll maximum near the nitracline, TTS — The euphotic zone is essentially a two-layer system, with a nutrient-depleted surface layer and deeper water in which light limits phytoplankton growth (Dugdale 1967). Primary production and chlorophyll concentration are maximal near the nitracline, the boundary between the two layers, where simple models of algal growth as functions of light and nutrient concentrations would predict. The chlorophyll maximum is maintained as a result of enhanced growth in a stratum. Steady-state models in the vertical dimension may be able to describe most of the chemical and biological features of typical tropical structure; input of nutrients to the euphotic zone by turbulence from below would be a very important term in any solution (cf. Margalef 1978; Kaiser and Postel 1979).

In highly structured systems such as those in the tropics, or

in temperate waters in the summer, sampling effort should be concentrated near the nitracline (chlorophyll maximum, thermocline) where parameters change most rapidly (cf. Herbland and Voituriez 1979). Especially when the relationships between phytoplankton and zooplankton profiles are being studied (cf. Mullin and Brooks 1972; Longhurst 1976; Longhurst and Herman 1981; Ortner et al. 1981) careful attention should be paid to determining the extent to which the distribution of chlorophyll reflects phytoplankton biomass (visual counts would be best, but particle counts, ATP analyses, or particulate C and N and P analyses would be useful).

Physiological adaptation of C:Chl — Some evidence indicates that C:Chl in deep chlorophyll maxima dominated by organisms other than dinoflagellates is about 25 (Eppley 1968; Beers et al. 1975; Cullen 1980), about what would be predicted from laboratory experiments. If the phytoplankton above the chlorophyll maximum is light-saturated and possibly nutrient-limited, C:Chl will be higher near the surface: about 100 in the Southern California Bight during the summer (cf. Eppley 1968; Cullen 1980; see also Steele and Baird 1962) and in the range of 150–250 in oligotrophic central gyres (Beers et al. 1975; Redalje and Laws 1981). These results strongly support the calculations of Steele (1964). Surely, when nutrient limitation is important near the surface, chlorophyll distributions can have little to do with phytoplankton biomass. Thus, attempts to relate zooplankton distributions to chlorophyll concentration may be confounded. The suggestion that zooplankton exploit preferentially the depth of maximum primary production and that chlorophyll profiles are to some extent determined by depth-differential grazing (Lorenzen 1967; Longhurst 1976; Herman et al. 1981), cannot be examined thoroughly until the proper measurements of phytoplankton biomass are made with sufficient spatial resolution, and the grazing rates of herbivores are related to the concentrations of food available to them.

Decrease in sinking rate of phytoplankton — As a purely physical process (cf. Derenbach et al. 1979), variations in sinking rate as a function of density structure may create phytoplankton patchiness that is important, or perhaps necessary (cf. Mullin and Brooks 1976) to survival of herbivores. More high-resolution measurements will tell us how common microscale chlorophyll maxima (Derenbach et al. 1979) are in nature, and what their temporal persistence is.

When a subsurface nitracline is present, sinking diatoms will aggregate on it (Steele and Yentsch 1960). If irradiance near the nitracline is conducive to growth, significant primary production will occur in that stratum (cf. Anderson 1969, 1972). To quantify important biological fluxes in a system with a "type 3" chlorophyll maximum, sinking rates above and below the maximum must be determined. Smayda (1970) has collected the best estimates, but measurements *in situ* (Bienfang 1980) would provide information directly applicable to specific profiles.

Behavioral aggregation of phytoplankton — If a chlorophyll maximum layer in stratified water is dominated by dinoflagellates or other motile phytoplankton, behavior should be considered as a mechanism of aggregation. Aggregations of dinoflagellates have been interpreted from several perspectives: Lasker (1975) suggested that a chlorophyll maximum layer dominated by *G. sanguineum* (= *splendens*) was a food resource critical to the survival of larval anchovies. P. C. Fiedler and M. Huntley (Scripps Institution of Oceanography, La Jolla, CA, personal communication) determined that herbivorous crustacean zooplankton had reduced feeding rates within a similar layer of the same organism, and stratified sampling indicated that several taxa of zooplankton avoided the layer. Fiedler and Huntley also demonstrated reduced feeding by *Calanus pacificus* on a bloom of *Gymnodinium flavum*, a dinoflagellate morphologically similar to *G. sanguineum* (= *splendens*). Resistance to grazing has likewise been suggested for the thecate dinoflagellate *Ceratium tripos* (Conover 1978; Falkowski et al. 1980). Wyatt and Horwood (1973) suggest that, independent of relative palatability, behavioral aggregation of phytoplankton will lead to reduced mortality from grazing.

Dinoflagellates grow relatively slowly (Falkowski et al. 1980; Chan 1980), so it follows that reduction of losses from both sinking and grazing would be important to their survival. Behavioral aggregation may facilitate these reductions. If herbivorous zooplankters do not exploit patches of dinoflagellates, interpretation of chlorophyll distributions is complicated further because not even phytoplankton biomass is an adequate measure of food available to herbivores. We need more determination of grazing rates on phytoplankton dominated by dinoflagellates.

Effects of Zooplankton on the Vertical Distributions of Phytoplankton

The mechanisms of chlorophyll maximum layer formation and maintenance presented so far explain vertical distributions of chlorophyll with no special consideration of grazing by herbivorous zooplankton. It would seem ludicrous to try to explain vertical distributions of phytoplankton without incorporating grazing, if it were not for the satisfactory results that have been obtained. Still, the question remains, what effect does the zooplankton have on chlorophyll profiles?

Longhurst (1976) analyzed profiles of zooplankton abundances from the eastern tropical Pacific Ocean and found that subsurface maxima coincided with the depth of maximum carbon fixation, above the chlorophyll maximum. He inferred that depth-differential grazing pressure could exist in such a stable system, and, as most of primary production is consumed by grazers (i.e. sinking is relatively unimportant), the upper boundary of the chlorophyll maximum could be maintained by herbivory. Herman et al. (1981) have made similar observations for water near the Scotian Shelf. However, as I have shown, most vertical profiles of chlorophyll can be accounted for by fairly well-understood processes without any special regard to grazing. Surely, more work is needed to help fit grazing pressure into the framework of vertical structure (e.g. Jamart et al. 1979; A. Herman and T. Platt, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). Especially useful would be detailed measurements of phytoplankton biomass to go with profiles of epiplankton abundance and chlorophyll. As soon as the true relationships between phytoplankton and zooplankton profiles are discovered and generalized, theoretical work that examines the implications of these relationships should be more

rapidly advanced.

Significant advances in the study of vertical distribution of phytoplankton (and zooplankton, nutrients, primary production) require more than just good measurement. Hypotheses must be formulated and tested (cf. Mullin and Brooks 1972; Longhurst 1976; McGowan and Walker 1979). Further, the hypotheses should reflect the state of our knowledge: it should not be assumed, *a priori*, that fluorescence represents chlorophyll, chlorophyll represents biomass, or even that biomass represents acceptable food for herbivores.

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Predation and Freshwater Communities. *Thomas M. Zaret. Yale University Press, New Haven, Connecticut. 1980. pp. xiv + 187. $15.00 (U.S.)*

The obvious importance of predation in aquatic ecosystems has led to increased study, and it is very timely that the rather extensive and scattered literature should be synthesized. Zaret attempts to do this in his small book, at least for freshwater communities (some illustrative marine examples also are brought in). The main emphasis is on limnetic communities, with less on littoral regions in lakes. Flowing waters are virtually ignored. These varying emphases are in part a reflection of the author's main interests, but in greater part of the relative lack of available information associated with the greater difficulty in obtaining reliable quantitative field information in littoral and lotic environments.

A sharp distinction is made between "gape-limited predators" (GLPs), in which the prey is seized and swallowed whole, and "size-dependent predators" (SDPs), where the prey is seized and either the contents of the prey sucked out or the prey chewed into smaller pieces before ingestion. GLPs are mainly fishes, while SDPs are principally such invertebrates as copepods, predaceous cladocerans, and aquatic insects. It is shown that GLPs preferentially select larger prey up to the limit of their ingestion capacity, and that they cannot take food particles larger than this maximum. On the other hand, SDPs have no such sharp upper size limit, but beyond a certain size the prey becomes increasingly more difficult for them to handle. Hence for GLPs the selectivity curve shows an increase of consumption with size up to the maximum, then a sudden decrease to no intake of larger sizes. In contrast, the curve of selectivity for SDPs is bell-shaped with a maximum at the largest size that can be handled efficiently, but continuing with a reduced intake for still larger sizes as well. Of course, the actual prey sizes selected depend also on the sizes of the predators; GLPs usually are larger than SDPs, and therefore as a rule take larger prey.

The effects of all of this on aquatic communities is extensive. When GLPs are numerous, the larger prey specimens that are consumed include some of the important SLPs themselves. Thus the zooplankton community in these circumstances comes to be dominated by smaller species. On the other hand, when SDPs are numerous and GLPs are unimportant or lacking, the larger zooplankton species are favored because the smaller species are consumed by the predators. Also, GLPs usually select prey by sight, whereas SDPs select by detecting water movements produced in the swimming of the prey. Therefore, when GLPs are abundant, vertical migrations, transparency, and inconspicuous eyes are advantageous for prey whose size might otherwise be suitable as food for the GLPs. Because of the importance to SDPs of their ability to handle their prey, spines, crests, and body shapes that are more difficult to handle are advantages for prey survival. Such adaptations by the prey are documented in Zaret's book.

After considering these things, and models based upon them, Zaret devotes his final chapter to a series of fertile suggestions for further study aimed at elucidating the numerous unsolved problems that abound in the field of study under consideration. These will be invaluable to a whole generation of investigators.

Zaret's book is both informative and easy to read, and is to be recommended to ecologists, particularly those working with aquatic organisms. Unfortunately the book was inadequately proof-read, so that there are numerous typographical errors, especially in the spelling of generic and specific names. Also there are some regretable "goofs," such as in Fig. 21b where the drawing is listed as *Bythotrephes* whereas in reality it is *Polyphemus*. On p. 130, limnetic habitats are spoken of as "unstructured, physically homogenous areas." The author forgets temperature stratification, regions of upwelling and sinking of water, Langmuir cells, etc. On p. 131, Breen and Mann's work in marine waters in Nova Scotia is spoken of as "tropical." Ctenophores are listed as toxic marine zooplankters (p. 148), but Halstead in his book on toxic marine organisms lists no ctenophores (perhaps Zaret intended to say cnidarians). In one of his suggested areas for future research in the last chapter, Zaret wonders (p. 145) why if copepods "use only tactile cues [sic] . . . what function is served by their compound eyes?" Could he have meant cladocerans rather than copepods? Figure 7 is confusing in that it is captioned as "Aquatic larva of *Chaoborus*," whereas it consists only of the head capsule and the dissected out pharyngeal basket (crop) of that animal. Inevitably, weaknesses such as these detract from the otherwise considerable value of Zaret's book.

CHARLES C. DAVIS

Department of Biology and Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Nfld. A1B 3X9

(R349)

Coastal Upwelling. *Edited by Francis A. Richards. American Geophysical Union, Washington, D.C. 1981. xiii + 529 p. $23.00 (U.S.)*

Coastal Upwelling is a compilation of 60 papers by 131 contributors. The book owes its raison d'être to the IDOE (International Decade of Ocean Exploration) International Symposium on Coastal Upwelling; however, as Dr Richards is quick to point out the book is not a true symposium proceedings volume. Some of the papers in the book were not presented at the meeting and some papers presented were not included in the volume. The papers were refereed.

Papers are included on all aspects of coastal upwelling, covering various disciplines, examining specific upwelling events from all over the world, and covering in depth all of the world's major upwelling regions.

Although I had looked forward to seeing this volume for some time, I was rather disappointed in it. I had hoped for a volume that would stand as a substantial review of this important subject, but I found instead a preponderance of short

papers many of which are based on good science that will probably be published elsewhere in greater depth. There certainly are some exceptions; Smith, for example, has a fine paper comparing the oceanographic structure of three upwelling areas: Oregon, N.W. Africa, and Peru. The differences are interesting because of fundamental physical differences imposed by latitude and topography. For example, we normally regard a shelf system to consist of a quasigeostrophic interior bounded, top and bottom, by Ekman layers. However, off N.W. Africa the shelf is typically 70 m deep and the upper and lower Ekman layers have scale thicknesses of 35 and 64 m, respectively, and so no geostrophic interior can exist. Hence it is not surprising that current structures are different off N.W. Africa, despite a general similarity in the forcing field.

Another paper that I found to be thoroughly fascinating was a discussion of equatorial upwelling by Voituriez. The paper revolves around an apparent paradox in the equatorial upwelling system; nutrients are upwelled in large quantities, light is not limiting, so why do we find such a low level of primary and secondary productivity? Other notable papers were as follows: Johnson presents a clear and useful analysis of weakly stratified coastal currents; Guillén and Calienes present an interesting paper reviewing the biological and chemical responses of a region subjected to El Niño; and finally Cushing has a fine paper on the Peruvian anchoveta stock.

Another paper, on the "Water exchange and the balance of phosphate in the Gulf of Cariaco, Venezuela," by Taizo Okuda was notable for a different reason. The paper describes the exchange processes of a Venezuelan Inlet that looks for all the world like a fjord undergoing periods of deepwater stagnation and renewal. The paper is excellent and I found it fascinating, but (especially considering the editor's prefatory remarks) I had to wonder what it was doing in this volume. As far as I could determine, it had nothing to do with coastal upwelling.

The volume is generally well presented; the printing is clear and the figures are reproduced accurately and legibly. However, I have a number of criticisms of an editorial nature. There are far too many errors in the book. The errors vary from trivial typos (e.g. "along the the continental shelf" on page 19) to typos that change meaning (e.g. Moody et al. are happy with a correlation coefficient of -0.07 on page 31, clearly a typographical error) and humorous errors (e.g. on page 87 we read about "a week of even four or five days"). However, I would like to mention a more serious error in a paper with which I was associated: a large section of text is displaced between pages 515 and 519. Because the displaced material begins after the end of one paragraph, and ends similarly, it is not a trivial matter to determine that an error has occurred and less trivial to determine how the paper should be reconstituted.

The book costs only $23.00 (U.S. funds) which is certainly a remarkably low price for a technical volume. I would not, however, purchase the volume for my personal collection; it is sufficient to know that at least one copy is available in the library. All marine libraries should have a copy of this book.

H. J. FREELAND

Institute of Ocean Sciences,
P.O. Box 6000,
Sidney, B.C. V8L 4B2

(R384)

Books received/Livres reçus[1]

February/février 1982

The Dynamic Environment of the Ocean Floor. *Kent A. Fanning and Frank T. Manheim. Lexington Books, D.C. Heath and Company, Lexington, Massachusetts and Toronto. 1982. x + 502 p. $47.95.* Sampling methods are reviewed; dynamic interactions between solid particles and water at the sea floor are described and quantified. There are sections on biological measurements, dissolved interstitial gases and trace metals, and hydrothermal processes. [R407]

Brain Mechanisms of Behavior in Lower Vertebrates. *Edited by P. R. Laming. Cambridge University Press, New York. 1981. ix + 318 p. $49.95 hardbound; $22.95 paperback.* Society for Experimental Biology Seminar Series 9. The book is divided into five parts; the first deals with general considerations of brain structure and function and the other four with specific biological functions such as sensation, appetite, and learning. It concentrates on teleosts and amphibians and how the brain controls their behavior. [R408]

Marine Fish Larvae: morphology, ecology, and relation to fisheries. *Edited by Reuben Lasker. Publisher, Washington Sea Grant Program. Distributor, University of Washington Press, Seattle. 1981. xiii + 131 p. $8.50 (U.S.).* The book, based on lectures given by Paul E. Smith, John R. Hunter, Reuben Lasker, and H. Geoffrey Moser at the University of Washington College of Fisheries in 1979, examines the second stage of the early life history of marine fish. Included are behavioral, physiological, and morphological characteristics that affect growth and survival, predator–prey relations, and the role of a stable ocean. [R409]

Trends in Fish Utilization. *J. J. Connell and R. Hardy. Fishing News Books Ltd., Farnham, Surrey, England. 1982. x + 105 p. £6.00 + 60p (postage/packing).* Those concerned with future trends in the use of marine resources as food for human consumption will be interested in this report based on the work of scientists at the Torry Research Station. The authors discuss authoritatively how fish and shellfish raw materials from the seas around Britain might be exploited more effectively. [R410]

Extended National Fisheries Jurisdiction: palliative or panacea? *Roy Jackson. Publisher, Washington Sea Grant Program. Distributor, Washington Sea Grant Communications, Seattle. 1982. v + 30 p. $3.00 (U.S.).* This is the third McKernan Lecture and concerns the problem of international management of fish resources, i.e., fish caught within national zones up to 200 miles offshore. After discussing the state of world fisheries today, the author explains what extended jurisdiction means to selected areas. [R411]

Stress and Fish. *Edited by A. D. Pickering. Academic Press Inc. (London) Ltd., England. 1981. xiv + 367 p. £24.60; $59.50.* Based on invited review papers of a symposium in late 1980 organized by the Fisheries Society of the British Isles, this book is aimed at those with an interest in fish cultivation and the development and maintenance of sport and commercial fisheries. The endocrinological/physiological responses of fish to stress are given particular attention. [R412]

Faune Tropicale: réquins de Méditerranée et d'Atlantique (plus particulièrement de la Côte Occidentale d'Afrique). *J. Cadenat et J. Blache. Éditions de l'Office de la Recherche Scientifique et Technique Outre-Mer (ORSTROM). Collection Faune Tropicale xxi. Paris. 1981. 330 p.* Il y a clés de détermination des familles, des études systématiques des Squalomorphes et Galeomorphes, une bibliographie, et plusieurs excellentes illustrations. [R413]

Poissons de Mer de l'Ouest Africain Tropical. *Bernard Seret (texte) et Pierre Opic (illustrations). Office de la Recherche Scientifique et Technique Outre-Mer (ORSTROM). Initiations–Documentations Techniques No. 49. Paris. 1981.* Cet ouvrage s'adresse au naturaliste amateur, au pêcheur sportif, au chasseur et plongeur sous-marins. La forme de présentation est celle du catalogue. Dans la plupart des cas, l'illustration suffit à reconnaître le poisson. Il y a une courte description de chaque espèce, les données sur la répartition géographique, l'habitat, la biologie et la pêche. [R414]

Aquarium Systems. *Edited by A. D. Hawkins. Academic Press Inc. (London) Ltd., England. 1981. x + 452 p. £27.80; $67.00.* This is a comprehensive guide to fish keeping in the laboratory. Consideration is given to the basic aspects of aquarium design and construction, the supply of aquarium water and its treatment, the problems of handling fish, the rearing of larval fish, and the culture of shellfish. The volume should be of interest to aquarists, fish farmers, and research scientists. [R415]

Fishes: an introduction to Ichthyology. *Peter B. Moyle and Joseph J. Cech, Jr. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 1982. xiv + 593 p. $29.95 (cloth).*

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[1]Persons interested in reviewing books in this list should contact the Book Review Editor, Canadian Journal of Fisheries and Aquatic Sciences, Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa, Canada K1A 0E6.

[1]Les personnes intéressées à examiner les livres énumérés dans cette liste sont priées de communiquer avec le Rédacteur des comptes rendus, Journal canadien des sciences halieutiques et aquatiques, Direction de l'information et des publications scientifiques, Ottawa, Canada K1A 0E6.

In large part the book is designed to serve as a text for classes in fish biology. The authors provide the balanced coverage necessary to understand how fish survive at the same time emphasizing function, classification, and ecology. Evolution, structure, physiology, ecology, and behavior are examined in detail. [R416]

Papers on the Fifth Symposium on Hudson River Ecology 1980. *Edited by Joseph W. Rachlin and Gilvert Tauber. The Hudson River Environmental Society. Produced by Publishing Center for Cultural Resources, New York City. 1981. 107 p. (paperback).* Proceedings of the symposium held on April 24 and 25, 1980. The theme was the effective use of the Hudson River as an integrated system with sessions on energy production, shoreline modification, water and wastewater, and fisheries. [R417]

ANNOUNCEMENTS/AVIS

Symposium on Acidic Precipitation and Atmospheric Deposition: A Western Perspective

The symposium, sponsored by the Center for Canadian–American Studies of Western Washington University, will be held June 24–26, 1982, at Bellingham, Washington. Sessions will be devoted to assessment of impacts of acidic precipitation in North America and Europe; atmospheric deposition patterns of acids, metals, and organics in western North America; and political and economic aspects of transboundary air pollution. A half-day workshop (June 26) will evaluate the present data base for the western U.S. and Canada and develop plans for cooperative research. A volume of proceedings of the meeting will be published.

For further information, please contact: *Dr David F. Brakke, Huxley College, Western Washington University, Bellingham, WA 98225, USA, (206) 676-3520 or 3502.*

Colloque sur les précipitations acides et la déposition atmosphérique : une perspective occidentale

Ce colloque, organisé par le Centre d'études canado–américaines de l'Université de Western Washington, se tiendra du 24 au 26 juin 1982 à Bellingham (Washington). Les séances porteront sur l'évaluation de l'impact des précipitations acides en Amérique du Nord et en Europe; les modalités de la déposition atmosphérique des acides, des métaux et des matières organiques dans l'ouest de l'Amérique du Nord; et les aspects politiques et économiques de la pollution atmosphérique transfrontière. Au cours d'un atelier de travail d'une demi-journée (26 juin) on évaluera la banque de données actuelle de l'ouest des États-Unis et du Canada et on élaborera les plans d'une recherche en collaboration. Les comptes rendus de la réunion seront publiés.

Pour plus amples renseignements, on est prié de s'adresser à : *Dr David F. Brakke, Huxley College, Western Washington University, Bellingham, WA 98225, USA, (206) 676-3520 ou 3502.*

Book Review Editor
Canadian Journal of Fisheries and Aquatic Sciences

We are seeking a volunteer for the position of Book Review Editor for a 3-yr term, effective immediately, to continue the Book Review section in the Journal. The individual will be responsible for keeping abreast of new publications in fisheries and aquatic sciences, occasionally soliciting review copies from publishers, obtaining and editing reviews of meritorious books, and preparing an annotated list of Books Received for the Journal. The editorship requires approximately $\frac{1}{2}$ day of an individual's time per week, and about $\frac{1}{2}$ day of clerical support for smooth flow of correspondence and record-keeping.

Interested persons should contact *Johanna Reinhart* at *Canadian Journal of Fisheries and Aquatic Sciences, Department of Fisheries and Oceans, Scientific Information and Publications Branch, 240 Sparks Street, 7th Floor West, Ottawa, Ontario K1A 0E6, (613) 996-1656.*

Rédacteur des comptes rendus
Journal canadien des sciences halieutiques et aquatiques

Nous recherchons actuellement un rédacteur des comptes rendus; la personne choisie sera responsable de la section "Comptes rendus" du Journal pendant les trois prochaines années. Elle devra se tenir au courant des nouvelles publications concernant les sciences halieutiques et aquatiques; se procurer, à l'occasion, des résumés auprès des éditeurs; obtenir et publier des résumés d'ouvrages méritoires et préparer une liste des livres reçus. Ces fonctions nécessitent environ une demi-journée de travail par semaine; il faut également compter une autre demi-journée pour répondre au courrier et tenir les dossiers.

Les personnes intéressées sont priées de communiquer avec *Johanna Reinhart, Journal canadien des sciences halieutiques et aquatiques, ministère des Pêches et des Océans, Direction de l'information et des publications scientifiques, 240, rue Sparks, 7e étage ouest, Ottawa, (Ontario), K1A 0E6, à (613) 996-1656.*

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